

THE PSYCHOLOGICAL BULLETIN

RECENT EXPERIMENTS ON THE FUNCTION OF THE FRONTAL LOBES

BY CARLYLE F. JACOBSEN

University of Minnesota

Theories of cerebral function have been numerous and varied, the interpretation of experimental findings being determined by psychological systems in vogue at the time, many of which systems have since been discarded. The history of the problem is full of contradictory results, futile speculations, denials and counterdenials. The advent of animal laboratories and of carefully controlled animal experimentation marked a turning point in studies of cerebral localization. Franz, publishing in 1907 the first well controlled experiment in learning and brain destruction, emphasized the need for better methods in the field of animal experiments. "The experiments which have been described and the results which have been obtained have, I think, value other than that of indicating the functions of parts of the association areas in animals. They indicate that for the determination of disturbances coincident with lesions in the association areas better methods of diagnosis and experiment are needed. The experiments show not only that there are changes coincident with lesions or disturbances of the frontal lobes but that the associational loss is one that could not be determined by simple observational methods." Since most of the early work lacked quantitative measurement of the learning performance, we shall, for the purposes of this review, be concerned chiefly with the work of the last ten years.

The earlier work on cerebral function has been reviewed by Soury (22), Franz (4), and Bianchi (1). Franz summarizes the work on the frontal lobes under four groups of functions: (1)

movement, (2) inhibition, (3) attention, (4) association. (1) Munk found that dogs exhibited paralysis of the trunk muscles following extirpation of the frontal lobes. Ferrier reported disturbances of eye and head movements. Sherrington and Grunbaum have confirmed Ferrier's findings. These results were not confirmed by the observations of Goltz, Horsley and Shafer, and Franz. (2) Shafer attributes an inhibitory function to the frontal lobes on the basis of a shortening of the time of spinal reflexes. This view has been criticized because of the inadequate measurement of reaction times, and also, because of the negative findings of other investigators. (3) Ferrier reporting paralysis of eye and head movements, and Langelaan and Beyerman observing irregular respiratory functions coincident with frontal destruction, accept a motor theory of attention, and assign this function to the frontal lobes. Franz criticizes this view on the grounds that "movements of attention are confused with attention itself." His findings do not support the contentions of Ferrier, Langelaan and Beyerman. (4) The association theories regard the frontal lobes as centers for "intellectual states." This interpretation is based on the clinical and experimental findings of a number of investigators, although results from these sources are not free from negative instances. Shafer and Horsley found no impairment of intelligence in monkeys following destruction of the frontal lobes. Goltz reported no interference when dogs were used as the subjects. Bianchi and Franz working chiefly with monkeys reported that deterioration of behavior attended removal of the frontal areas. This summary is condensed from Franz' above-mentioned article.

The work of Franz presents a new approach to the problem of cerebral localization. To the usual descriptive account of the animal's general behavior, he added observations on cats and monkeys trained on problem boxes requiring the formation of definite motor habits. The time and number of trials required for learning before and after operation furnished a quantitative basis for judging the effects of extirpation of brain tissue. The cats were trained to escape from boxes by pulling at strings and turning buttons. The monkeys were trained on the button box and the hurdle which involved climbing over a box, through a hole, up and down two short ladders, and finally opening a box to obtain food. Following the acquisition of these habits, Franz severed the area anterior to the precentral sulcus (in monkeys) by inserting a small scalpel which

left the destroyed tissue *in situ*. He found that the ablation of the indicated areas resulted in the loss of the newly acquired problem box habits, although, in some instances, habits of long standing were retained. Further, in certain animals the removal of the frontals did not result in the loss of the habit. These negative instances and the retention of long-established habits he explained in the following manner. The frontal lobes functioned in the acquisition of the habits, and with repetition the pathway became shortened, the lower centers being concerned with the coördination of the sensory-motor elements. This reduction to lower centers seems to be a questionable interpretation in the light of more recent work by Franz and Lashley (7) and Lashley (13). These investigators trained rats on the maze and on the latch box to determine whether long-continued practice would reduce the organization to subcortical levels. The maze habit showed no localization at any stage of learning and survived destruction of the frontal regions. The maze habit, however, was localized in the frontal regions. Complete destruction of this area abolished the habit in spite of training to three times the amount necessary for acquisition; on the other hand, partial destruction was followed by retention of the habit. Lashley trained animals in a visual discrimination problem. This habit was abolished by the destruction of pathways in the occipital region although the animals had received more than a thousand trials after learning the problem. However, kinesthetic motor adjustments were retained. He concluded that long training did not reduce the habit to subcortical levels. Because of differences in the problems used and differences in the motor functions in the rat and in the monkey, these results are suggestive rather than conclusive on the point in question. It is perhaps significant, in the light of the later emphasis upon the mass function of the cerebrum, that Franz reported that the extirpation of one frontal area does not always result in the loss of the habits. In a control experiment in the cat series Franz has shown that surgical shock attendant upon the operation, up to, but not including the removal of cortical tissue produces no loss of efficiency in performance. Likewise, destruction of equal amounts of tissue in other parts of the cortex does not produce interference. Hence, the loss of habits following destruction of the frontals is not to be explained on the basis of surgical shock, loss of blood, or even the shock attendant upon the ablation of brain tissue itself. Since reacquisition of the lost habit is possible after the removal of the frontals in about

the same length of time as that required for the original learning, Franz concluded that although the frontals functioned in the acquisition of new habits, learning may still occur in their absence. Franz reported no marked emotional changes following the operations in either cats or monkeys—"any change present, particularly in cats, was in the direction of greater friendliness." Emaciation and liability to disease were noted in the cats but not in the monkeys.

Following the initial work of Franz there have been numerous studies of a similar character. Franz and Lashley (7) trained a group of rats in a maze fashioned after the Yerkes discrimination box, requiring the establishment of a position habit of turning to the right. There was clear evidence of retention following the removal of large parts of the frontal portions of the cerebrum. The animals did not show the typical exploratory behavior in retests on the maze, although they did do so when placed in new situations.

In a subsequent article Franz and Lashley (11) extended their researches to include destruction of the frontal-temporal and frontal-parietal areas in rats which had been trained in the simple maze problem. They concluded that "no part of the cortex in front of the caudal end of the corpus callosum and above the level of the floor of the lateral ventricles is concerned with the retention of simple kinesthetic-motor habits." The inclined plane box was selected as a suitable problem since it combined specific reactions to stimulating objects with a relatively complex motor response. Animals in which the frontal pole was removed before training succeeded in learning this problem in normal time. Seventeen of the normal animals trained on the inclined plane box survived operations in the frontal region. Destruction of large areas in this region resulted in the loss of the habit, although destruction of smaller areas produced only a partial deterioration. In the course of the experiments all parts of the frontals were destroyed although there was not complete destruction in any single animal. For the retention of this habit it is necessary that some part of the frontal region remain intact, although the particular part preserved is immaterial. The authors conclude that "the different parts of the frontal area are, to adopt a term from experimental embryology, equipotential in the functioning of the habit." Another group of rats suffered very extensive injuries to the cortex. The animal with the most extensive lesions in the frontal and temporal regions failed to exhibit the normal exploratory behavior so that training in the ordinary laboratory

situations was not possible, yet this animal did give evidence of the ability to form simple habits to food situations. Attempts to establish a conditioned reflex in this animal were unsuccessful. Other animals with the destruction of one-third to one-half of the cortex gave "clear evidence of some degree of habit formation." The authors interpret their results as "going far toward establishing the complete functional interchangeability of all parts of the cerebral cortex."

In the consideration of the frontal lobes as a "locus of intelligence" the work of Bianchi, published over a period of years and summarized in his recent book on cerebral function (1) should be mentioned. He reported marked deterioration following the removal of the prefrontals. Monkeys thus operated show:

1. Defects of perceptive power. The animal is unable to distinguish pieces of chalk from pieces of banana, and is unable to distinguish a real threat from a pretended threat of the attendant.

2. Weakness and unreliability of memory which is reduced for both old and new acquisitions. The monkey is unable to utilize past experience, shows less variability of behavior persisting in the repetition of futile responses. He can be fooled readily with cherries dipped in quinine although the normal monkey would be suspicious.

3. Reduction of associative power. The monkey, which sees a door handle, does not attempt to turn it to open the door, but sits on the handle. "Evidently there are lacking those images that are necessary for the determination of a series of movements coördinated towards one end."

4. Modification of the emotions and sentiments. Primitive emotions, desires for satisfaction of hunger, thirst and other organic needs, persists; the change occurs in the higher sentiments such as friendship, gratitude, protection, etc. The whole psychic tone is lowered. The animal is sloppy in appearance, sex drive is lowered or lacking. Tics and stereotypes, characteristic of the feeble-minded, are shown in several of the histories of mutilated animals. Bianchi emphasizes the necessity for bilateral destructions to produce the described results.

His studies are deficient in several respects—quantitative measurement of the deterioration is lacking, and there is a failure in many instances to confront the animal with the same situations following the operation, which fact makes impossible a comparison of pre- and post-operative behavior. To the reviewer Bianchi's inter-

pretations of the animal's behavior in terms of "instinct of decency," "sense of shame" (over the sex act), "premeditation" and the like offer considerable difficulty to the acceptance of his conclusions.

Bianchi's chief emphasis is on the abstract intellectual function of the frontal pole, but "for this view," Herrick (8) states, "there is no adequate foundation" (p. 231). Herrick stresses the premotor function of the cortex with its significance for behavior patterns. "A part of this is the organization of efferent cortical discharges into the specific synergic patterns necessary for the phasic control of intentionally directed effort . . . This function is represented in the frontal lobes of all mammals, . . . The apparatus in question lies in the intermediate precentral field just in front of the excitable areas." Dr. K. S. Lashley and the writer have repeated Bianchi's experiment and have failed, for the most part, to verify his findings. Monkeys which were trained on complex manipulatory and sensory problems failed to show deterioration of these habits following destruction of the precentral area. These results make questionable Herrick's interpretation of the frontal function as one of premotor organization, or at least, they indicate that there must be other such premotor areas. On the basis of the intimate anatomical connections between the thalamus and the extreme prefrontal cortex (only rudimentary in the monkey although well developed in the human) and on the basis of clinical findings of emotional disturbance following injury to the prefrontals, Herrick suggests that this area may be concerned with affective components of behavior. Bianchi reported positive results on this point; Franz, positive in the case of cats, negative in the case of monkeys. Stone (23) studying the effects of cerebral destruction on sex behavior, which presumably involves affective elements, found negative results. It should be mentioned that in dealing with emotional behavior of the animal we still lack an objective criterion of emotionality, and that we probably will be unable to answer this question until we obtain such a criterion.

A recent contribution to the function of the frontals is that of Hunter (9) who trained animals on the double platform box described by Lashley. Training was followed by operations producing lesions in the frontal, temporal, parietal, and occipital areas. Six of the seven animals with lesions in the frontal region showed deterioration of the habit when there was destruction of more than 6.5 per cent of the neopallium. The animal with the slightest lesion (6.5 per cent) showed no loss of the habit. Hunter indicated that

for this frontal group there were quantitative differences. Animals with lesions outside the frontal areas showed no constant interference with the habit. The average number of trials required for animals with lesions outside the frontal region was one-half that of the standard, while for animals with lesions in the frontal area the average was twice that of the standard. She also found evidence that animals retained their general orientation to the problem situation although the specific habit involved was lost.

The literature on the function of the so-called motor area of the frontal lobe presents a similar disparity of results. The trend of the later results has been away from the strict point for point correspondence. The recent work can be divided into rather overlapping classes, the first dealing with stability of function for a particular point, the second with significance of the motor areas in learning.

Franz (6) mapped the excitable areas in a number of rhesus monkeys and reported that there was considerable variation in the localization of stimuable points from individual to individual, and also from one hemisphere to the other in the same brain. He concluded that "connections made by way of the cortical motor cells are not definite in the sense, for example, that there is the passage of an impulse from a Betz cell in the anatomically defined cerebral motor region." He emphasized the probable absence of strict anatomical correspondence between cortical and spinal motor centers, and wrote "the impulses resulting from the activity of a cell body may affect many other cells." Stout (24) employing a similar technique mapped the motor areas in cats, and found a like variation in function. He indicated also a relationship between the frequency and the wide distribution of points producing a particular type of movement and the need for that movement in the animal's adjustment. Leyton and Sherrington (20) working on higher primates have corroborated Franz' results on variation. They concluded that there was a broad localization which followed a topographical distribution but that more minute localization showed an instability "which is largely the expression of mutual influences exerted transiently by the physiological states of different points of the cortex." Brown and Sherrington (3) reported the reversal of function for the same point, stimulation now producing extension, later causing contraction of the same muscle group. Lashley (19) mapped the excitable area in the monkey in a series of tests. Within the same test period he found almost constant reactions. In different test periods the general

fields for muscle groups were fairly constant although the borders of the field were inconstant. Within the arm area, stimulation at different times of the same point produced widely different movements, and stimulation at different times of widely separated areas produced the same movement. Extreme fatigue failed to modify the character of the movements elicited from the stimuable regions. He interpreted his results as justifying the abandonment of the concept of strict anatomical localization, and concluded that "within a segmental area the responses obtained on electrical stimulations are due to the temporary physiological condition and do not give evidence for a corresponding structural differentiation."

In a study on the function of the stimuable area and caudate nucleus in the rat, Lashley (14) has shown that neither of these structures, which probably correspond in function to the excitable cortex in primates, are necessary for the acquisition of simple somesthetic-motor habits. Animals which were trained in visuo-motor and somesthetic-motor habits showed clear retention following the destruction of the indicated structures. One of the chief symptoms attendant upon injury to the stimuable cortex and caudate nucleus was difficulty in assuming new postures. Once an activity had been initiated it might continue for some time until a stimulus to a new posture occurred. Lashley suggested that the primary function of the cerebral motor mechanisms in the rat is the regulation of postural reflexes.

Lashley (16) has summarized the various views on the rôle of the stimuable areas in the learning process in the following manner: "Stated objectively, three mutually incompatible theories concerning the function of the precentral gyrus are to be found in the current literature. They are: 1. This area is the only centrifugal outlet from the cerebral cortex for complexly integrated movements, or for movements acquired as the result of training. 2. In the intact animal, the Betz cells are the principal centrifugal paths, but some neural impulses of like function may descend by extrapyramidal tracts, and these tracts may assume vicariously all the functions of the motor area. 3. The motor area is a part of the mechanism functioning in the regulation of tonus and posture and is not directly concerned in conditioned reflex activity." The first hypothesis is disposed of by the evidence for habit formation after the destruction of the excitable areas—Franz and Lashley (11), Lashley (12) and Jellinek and Koppanyi (10), and others.

Lashley's (16) experiment was designed to throw light on the last two hypotheses. Monkeys were trained on a series of problem boxes and on the visual discrimination of cubes of banana from wooden cubes. The motor areas were then destroyed. Following recovery from the ensuing paralysis the animals, again tested on the problem boxes, gave clear evidence of the retention of the habit after the loss of the motor area. The performance of a problem box which had been originally learned with the right side was later shifted to the left side when the right was paralyzed. He concluded that the "so-called motor areas are not directly concerned with the performance of complex learned activities" but that it is rather to be considered as a part of the kinetic mechanism for reflex control of spinal posture and for the maintenance of excitability of lower motor centers. This interpretation of the function of the cerebral motor structures would make them an additional link in the series of spinal, vestibular, and cerebellar mechanisms for the regulation of postural reflexes which have been described by Wilson (25).

Finally, mention should be made of the present trends in the problem of cortical localization as indicated by the recent paper of Lashley (18) and the contribution of Herrick (8) in which he summarizes in considerable detail the anatomical development of the cortex, reviews extensively the literature and reinterprets some of Lashley's findings.

Lashley, as part of an extensive program including experiments with animals higher in the evolutionary scale, trained rats in the visual discrimination box. Group A suffered removal of from 3.5 to 43.9 per cent of the visual areas before training. This destruction did not retard the rate of acquisition of the habit, nor did it increase the variability of the operated animals in comparison with that of normal animals. Groups B and C were trained in the discrimination box and were then subjected to occipital injury. Lesions ranged from 1.5 to 31.9 per cent of the neopallium. Animals with slight destruction showed little or no loss, while animals with extensive injury often required complete retraining in the habit. The correlation between relearning and extent of lesions for this group was $+71$. There is no support for the existence of a focal point in the visual area which has special significance for the visual function [Cf. Hunter (9)]. On this point Lashley writes, "The quantitative data point to the conclusion that the efficiency of the memory trace is proportional to the amount of functional tissue, irrespective of

its locus, and this in turn suggests that the function of the memory trace must in some way be additive, efficiency increasing as a simple function of the mass irrespective of the neural patterns involved." "This summation takes place in spite of the cutting of any particular group of association fibers. From this it is argued that the theory which makes the conditioned reflex arc the unit of cerebral organization is inadequate, and that an additional cerebral mechanism permitting greater plasticity of action and resembling in its action the syncytium of the lower invertebrates must be postulated." Although Lashley's interpretations are based primarily on data for visual habits, they will not be without significance for the frontal areas.

BIBLIOGRAPHY

1. BIANCHI, L., *The Mechanism of the Brain and the Function of the Frontal Lobes*. (Trans. by J. H. MacDonald). E. & S. Livingstone, Edinburgh, 1922.
2. BROWN, T. G., The Motor Activation of Parts of the Cerebral Cortex Other Than Those Included in the So-called "Motor" Areas in Monkeys, With a Note on the Theory of Cortical Localiation of Function. *Quart. J. Exp. Physiol.*, 1916, 10, 103-144.
3. BROWN & SHERRINGTON, On the Instability of a Cortical Point. *Proc. Royal Soc.*, 1912, B 85, 250.
4. FRANZ, S. I., On the Functions of the Cerebrum: the Frontal Lobes. *Arch. of Psychol.*, 1907, No. 2, 1-64.
5. FRANZ, S. I., On the Functions of the Cerebrum: the Occipital Lobes. *Psychol. Monog.*, 1911, 13 (No. 56), pp. 1-118.
6. FRANZ, S. I., Variations in Distribution of the Motor Centers. *Psychol. Monog.*, 1915, 19, 80-160.
7. FRANZ, S. I., and LASHLEY, K. S., The Retention of Habits by the Rat After Destruction of the Frontal Portion of the Cerebrum. *Psychobiol.*, 1917, 1, 3-18.
8. HERRICK, C., *Brains of Rats and Men*. Univ. of Chicago Press, 1926.
9. HUNTER, D., Masters Thesis on File in the Library of the University of Minnesota (June, 1926).
10. JELLINEK, A., and KOPPANYI, T., Lernfahigkeit gehirnverletzter ratten. *Akad. Wissen. in Wien, Akad. Anz.*, 1923, No. 17.
11. LASHLEY, K. S., and FRANZ, S. I., The Effects of Cerebral Destruction Upon Habit Formation and Retention in the Albino Rat. *Psychobiol.*, 1917, 1, 71-140.
12. LASHLEY, K. S., Studies of Cerebral Function in Learning. *Psychobiol.*, 1920, 2, 55-135.
13. LASHLEY, K. S., Studies of Cerebral Function in Learning. II. The Effects of Long Continued Practice Upon Cerebral Localization. *J. Comp. Psychol.*, 1921, 1, 453-468.
14. LASHLEY, K. S., Studies of Cerebral Function in Learning III. The Motor Areas. *Brain*, 1921, 44, 255-386.

15. LASHLEY, K. S., Studies of Cerebral Function in Learning IV. Vicarious Function After Destruction of the Visual Areas. *Amer. J. Physiol.*, 1922, **59**, 44-71.
16. LASHLEY, K. S., Studies of Cerebral Function in Learning V. The Retention of Motor Habits After Destruction of the So-called Motor Areas in Primates. *Arch. of Neurol. and Psychiat.*, 1924, **12**, 249-276.
17. LASHLEY, K. S., Studies of Cerebral Function in Learning VI. The Theory that Synaptic Resistance is Reduced by the Passage of the Nerve Impulse. *Psychol. Rev.*, 1924, **31**, 369-375.
18. LASHLEY, K. S., Studies of Cerebral Function in Learning VII. The Relation between Cerebral Mass, Learning, and Retention. *J. Comp. Neurol.*, 1926, **41**, 1-48.
19. LASHLEY, K. S., Temporal Variation in the Function of the Gyrus Precentralis in Primates. *Amer. J. of Physiol.*, 1923, **65**, 585-602.
20. LEYTON and SHERRINGTON, Observations on the Excitable Cortex of the Chimpanzee, Orang-utan, and Gorilla. *Quart. J. of Exp. Physiol.*, 1917, **11**, 135-222.
21. ODEN, R., and FRANZ, S. I., On Cerebral Motor Control: the Recovery from Experimentally Produced Hemiplegia. *Psychobiol.*, 1917, **1**, 33-49.
22. SOURY in Richet.
23. STONE, C. P., The Effects of Cerebral Destruction on Sexual Behavior of Rabbits. II. The Frontal and Parietal Regions. *Amer. J. of Physiol.*, 192, **72**, 372-385.
24. STOUT, J. P., On the Motor Functions of the Cerebral Cortex of the Cat. *Psychobiol.*, 1917, **1**, 177-229.
25. WILSON, S. A. K., An Experimental Research Into the Anatomy and Physiology of the Corpus Striatum. *Brain*, 1913-14, **36**, 427-492.

SOME EFFECTS OF INANITION ON ANIMAL BEHAVIOR

BY CALVIN P. STONE AND STANLEY LINDLEY

Stanford University

During the present century there has been a growing interest in types of inanition experimentally produced and associated with the *deficiency diseases* in animals. This interest already awakened was greatly strengthened by the nutritional adaptations necessitated by the World War. Owing to the nature of the subject, however, early researches dealt primarily with physiological and structural disturbances rather than alterations in mental development or changes in overt behavior.

The term *inanition* as herein used means the lack of essential food or food-stuff for time intervals considerably longer than those normally falling between feeding periods. Thus its scope is somewhat broader than the term *starvation*, which in current usage most frequently indicates an extreme stage of inanition leading to great emaciation and death.

As to character, Jackson (8) distinguishes two classes of inanition: (1) total, or quantitative inanition, in which there is absence or insufficiency in amount of food-stuffs; and (2) partial, or qualitative inanition, in which there is absence or insufficiency of one or more of the essential elements of the required food-stuffs. The duration and severity are distinguished by the terms: (1) acute, which is usually severe and of short duration, and (2) chronic, which is mild and of relatively long duration. The various types of inanition are summarized in the following table:

TYPES OF INANITION (AFTER JACKSON, 8)

I. Total (quantitative)

1. Complete (no food whatever)
2. Incomplete (insufficient nutriment; general underfeeding)

II. Partial (qualitative)

- | | | |
|------------------------|--|---|
| 1. Complete absence of | { one or more of
the necessary
food-stuffs | { proteins
fats
carbohydrates
salts
vitamins
water |
| 2. Insufficiency of | | |

EFFECTS OF INANITION ON GROWTH AND DEVELOPMENT

Jackson's book (8) dealing with the effects of inanition and malnutrition on growth and structure is almost encyclopedic in scope and reviews the early and recent literature on inanition in man and the lower animals. It has a bibliography of 107 pages. Among the facts most interesting to psychologists are those pertaining to the dystrophic growth resulting from chronic inanition. When the animal is in this state, certain tissues are more able to appropriate the available nutriment than others, hence *abnormal dissociation* of growth rate may follow. The skeleton is particularly resistant to general inanition, but is especially susceptible to certain types of partial inanition such as those associated with rickets and scurvy. In respect to resisting general inanition, the central nervous system is like the skeleton, but it, too, is affected by certain types of partial inanition as in beri beri and pellagra. The skeletal musculature, on the other hand, exhibits marked retardation or atrophy in the young and undergoes rapid atrophy in the adult as a result of either general or partial inanition. Especially susceptible are the reproductive tracts of both the male and female. Among the more prominent signs of its defects are delayed pubescence, sterility, and suppression of the *libido sexualis*.

In view of the striking and immediate effects of inanition during the post-natal life of infants, it is surprising to find that the embryo and foetus suffer only slightly, if at all. Apparently, they secure the requisite amount of nutriment at the expense of the mother. When she is no longer able to supply this amount the unborn young is eliminated by abortion.

Other recent books dealing with the experimental literature of inanition and malnutrition are those of Hess (5), McCollum (9), and Mendel (10).

AVOIDANCE OF INANITION THROUGH CHOICE BETWEEN
ADEQUATE AND INADEQUATE DIETS

That animals do choose between various food-stuffs when living in their native habitat is admitted by all, yet there is still some doubt as to whether animals can choose advantageously when there is a limited amount of food-stuffs available. Mitchell and Mendel (11) have made an extensive study of this problem with rats and mice and have brought forward evidence of a positive nature. Their experiments cover two types of investigations: (1) choice of adequate

and inadequate synthetic diets; and (2) choice of natural food-stuffs. *Normal growth rate was taken as the criterion of ability to select the adequate diet.* Only two possibilities of choice were offered an animal at a time, and attempts were made to keep alike the appearance and consistency of the two food-stuffs. A series of experiments using synthetic diets gave the following results:

a. Rats given the choice between foods high (18 per cent) and low ($4\frac{1}{2}$ per cent) in protein grew at practically normal rates; mice, likewise, when offered high (31 per cent) and low (7 per cent) protein diets closely approximated the normal growth rates. Although both food-stuffs were eaten, the superior diet was consumed in much greater quantities than the inferior diet. Previous experiments had demonstrated that the low protein diets were inadequate to promote normal growth.

b. When given the choice between two foods containing 18 per cent of casein (complete protein) and 18 per cent of zein (incomplete protein) rats grew at practically normal rates. Although they partook of both diets, the casein diet (complete protein) was consumed in much greater quantity. This, it was inferred, was necessary to supply the required amino-acids in which zein is notably deficient. Mice given a similar choice usually selected advantageously, but two of the group failed to select properly and showed a weight decline as was to have been expected in consideration of their eating a preponderant amount of the zein mixture. When later these two were put upon the casein mixture alone, they showed capacity for normal development. They were the only exceptions to the rule of advantageous selection of food-stuffs.

c. Experiments with foods rich and poor in vitamin A led to indecisive results because even the inferior food contained enough of that accessory to maintain a rat in fairly good condition throughout the period of the experiment. With mice, however, the results were not equivocal. Two young mice selecting the vitamin-rich food closely approximated the normal growth rate; one adult chose adequately for maintenance and slight growth although its choice involved a greater proportion of the vitamin-poor diet. Controls that were fed the inferior mixture exhibited a nutritive decline from which one subsequently recovered upon being fed cod-liver oil (rich in vitamin A) and the other, which could not be induced to take the oil, died.

d. A difference in the consistency of two food-stuffs rich and

poor in vitamin B complicated the interpretation of the next experiment. A protein-free milk used to supply vitamin B in the superior diet caused intestinal irritation and diarrhea when eaten in considerable amounts. Aside from the vitamin deficiency the other diet was a satisfactory and palatable mixture. At the outset the animals chose proportionally more of the inferior mixture, but soon when the vitamins stored in their bodies became exhausted they began to select greater amounts of the superior diet. Shortly after the beginning of the experiment, a decline in growth rate was apparent. This the authors attribute to the diarrhea producing superior diet. At the end of 10 weeks, the deficiency of the inferior mixture was rectified by daily addition of 0.2 gram of yeast apart from the diet. Thereafter, the animals selected proportionally more of the inferior food-stuff and their growth rate at once increased. This experiment demonstrated not only that the rats could select a food-stuff that supplied vitamin B, but also that they could discriminate between two adequate diets, one of which was probably "distasteful and irritating." Mice tested with food mixtures high and low in vitamin B, in which the vitamin of the superior food was supplied by yeast incorporated in the mixture, grew normally and thereby demonstrated ability to select the food-stuff which supplied the necessary vitamin. Although partaking of both, they chose proportionally more of the superior diet.

e. Both rats and mice when offered foods of high and low inorganic salt mixture chose adequately from the two to produce growth rates slightly above the normal. When they were restricted to the low-salt food, a decline in weight occurred. Animals reared from infancy on the low-salt diet showed marked retardation of their growth rates.

f. Rats offered ground whole corn, dry meat meal, and a salt mixture chose from these three supplies the requisite amounts for normal growth rates. Although the actual quantity of meat consumed was not large, the amount was sufficient to supplement the corn meal as to protein requirement; fed on corn alone, an animal grew less well. On the whole, this entire series of experiments confirms the earlier results of Osborn and Mendel (12) to the effect that rats and mice can and do make selection from food mixtures which are advantageous for their nutritive condition.

PERVERSIONS OF APPETITE

Green (4) reports many perversions of appetite in animals arising from faulty dietary regimes. Although some of the observations

have not been checked by rigidly controlled experiments, others are the direct results of scientific observation. Sheep that were fed a ration consisting of maize endosperm and a minimal ration of autoclaved hay (a diet faulty in both mineral and vitamin content) developed the wool eating habit and nibbled at one another continuously when brought into the yard. Although this habit is sometimes associated with skin parasites, in this case the author believed that the faulty diet was directly responsible for the prevalence of wool eating. Among the many perversions mentioned by Green, bovine osteophagia, a disorder prevalent in South Africa, has been subjected to the most rigidly controlled experimentation. It is a disorder resulting from phosphorous deficiency.

Cattle deprived of phosphorous show structural evidences of malnutrition and spend much of their grazing time searching for bones. A rough grading of the strength of the perversion was made by displaying in troughs available to the animals the clean, dry, weathered bones and bones with putrefying flesh adhering. With animals having only mild osteophagia, only the former were consumed, but with the more advanced states even the decaying flesh did not serve as a deterrent. Green states that a small proportion of cattle having the malnutrition characteristic of osteophagia never develop the bone eating habit and that a small proportion retain the habit even though force fed large quantities of bone meal. The great majority, however, react to the deficiency or supply of phosphorous compounds with great delicacy. Formation of the habit of bone eating by cattle is not understood although when once acquired the animals select this food-stuff in preference to an equally accessible supply of precipitated calcium phosphate or other unfamiliar sources of utilizable phosphate. Young cattle brought up on a phosphorous deficient soil from which bone debris was carefully removed manifested osteophagia the first time bones were displayed before them. This indicates that individuals may acquire the habit without imitating the actions of the herd. Any liberal ration of phosphorous compounds leads to rapid disappearance of the perverted appetite in most cases and, if regularly fed, prevents its appearance in young animals. If the perverted appetite is cured by feeding a phosphorous ration it appears again in a short time when the ration is temporarily withheld.

Slonaker and Card (15) observed that in a colony of rats maintained slightly over 8 years on a strictly vegetable diet there was a

greater tendency to eat the young than was found in another colony maintained on this same vegetable diet to which was added semi-weekly from 2 to 3 grams of animal protein.

INANITION AND SPONTANEOUS ACTIVITY

The probability that spontaneous activity in rats is reduced by chronic inanition arising from a deficiency in animal protein has been suggested by Slonaker (14). Two groups of four animals each were put into revolving cages soon after weaning and kept there during the remainder of their lives. One group, called the vegetarians, was fed liberally on a mixed table scrap diet composed primarily of vegetables or products of vegetables; the others, known as the omnivorous feeders, were given some meat each day in addition to the vegetables. His results clearly indicate a difference in the activity of the two groups throughout their life spans. The omnivorous females did approximately $9\frac{1}{2}$ times as much work in the revolving cages as the vegetarians, and the omnivorous males did almost $3\frac{1}{2}$ times as much as the male vegetarians. Senility appeared in the vegetarians much earlier than in the omnivorous feeders. The drop in the activity curves marking the approach of senility appeared earlier in life in the case of the former than in the case of the latter.

At the time of Slonaker's experiment he assumed that the animal protein consumed by the omnivorous feeders accounted for their greater activity and longevity. In view of the more recent data on nutritional requirements of rats, however, his results may not be confirmed upon repetition of the experiment. Slonaker's experiment has been repeated, in part, in a recent study by Hitchcock (6). This experimenter contrasted the activity of two groups of rats confined in revolving cages when one was fed a well balanced diet containing no meat, but having sufficient protein from another source (casein) for normal growth and maintenance, and the other was given a liberal allowance of meat in addition to the standard diet. Before differentiating the foods of the two groups, he put each animal into a revolving cage for one month to get a rough measure of its normal activity. On the basis of these results animals of approximately equal cage activity were paired. The experiment continued for periods of from 10 to 12 months with the net result that the activity curves were practically the same. Differences appearing were small and inconstant, hence he concluded that the absence of animal protein in the form of meat does not result in chronic inanition if the animals

are given an adequate supply of protein from other sources. Thus, in so far as this duplicates Slonaker's experiment, the results of the latter are not substantiated.

EFFECTS OF ACUTE INANITION ON DRIVE

According to Jackson (8) adult rats living on a strictly water diet succumb from starvation when they have lost about one-third of their normal body weight. Although changes in behavior associated with total inanition have not been extensively studied, there are sufficient data at hand to indicate that the hunger drive at different stages of total inanition varies and may be quantitatively measured. Richter (13) found that the activity of rats supplied only with water increased during the first 48 to 72 hours, but thereafter steadily decreased to a point of almost complete inactivity by the eighth day. Animals deprived of both food and water became progressively less active from the beginning and totally inactive on or about the fifth day.

Holden (7) using a modified form of Moss's obstruction method, in which the strength of an animal's drive is measured in terms of its willingness to undergo electrical shocks to secure a reward, studied the strength of the drive of acute inanition in the white rat. His problem had two objectives: first, to measure the strength of drive with advancing stages of acute inanition when the electrical shock was held constant; and second, to determine the relative effect of three different degrees of electrical shock upon the drive associated with advancing stages of inanition. His results indicated that the hunger drive increased during the first 12 to 36 hours after feeding and decreased with further extension of the duration of inanition up to 72 hours. As measured by the number of times the animals underwent the shock to get food the inanition drives at 12 to 60 hours and those at 24 and 48 hours were approximately equal. The number of animals immediately conditioned to avoid the grill reached its maximum at 36 to 48 hours of inanition and remained fairly constant from this point to 72 hours. In the second problem it was found that only the lowest degree of electrical shock used proved suitable for studying the hunger drives. Stronger shocks aroused conflicting tendencies which tended to obscure the hunger drive. According to Holden, animals appeared to be at the point of physical exhaustion at the end of 72 hours of starvation.

EFFECTS OF INANITION ON ANIMAL BEHAVIOR ASSOCIATED
WITH THE REPRODUCTIVE FUNCTIONS

There is now an extensive literature on the effects of inanition on the reproductive functions of a great variety of laboratory animals. From the standpoint of structural disturbances the most comprehensive review of the subject is given by Jackson (8). From the physiological point of view, the books of McCollum (9), Mendel (10), and the review by Marshall (8a) give an excellent orientation in the literature of this subject. Since disturbances in overt sex behavior are essentially alike, irrespective of the type of inanition, and vary only with its severity and duration a relatively small number of recent experiments will serve to illustrate the alterations observed.

Evans and Bishop (2, 3) showed that the sexual receptivity in female rats can be retarded as to age of first appearance, held in a state of dormancy subject to later revival, prevented from appearing throughout the lifetime of the individual, or in other ways manipulated in predictable manner by effective control of the daily dietary regime. The effects of quantitative restriction are illustrated by the following experiment. Three groups of littermate females were given a well balanced diet consisting of a mixture of whole wheat (67.5 per cent), casein (15 per cent), whole milk powder (10 per cent), calcium carbonate (1.5 per cent), sodium chloride (1.0 per cent) and butter fat (5 per cent). One group was allowed to reach a weight level of approximately 200 grams, another 125-150 grams, and a third but 60 to 85 grams. The most seriously stunted group did not show a single oestral cycle during the observation period of 325 days; in the less seriously restricted group 8 of the 10 animals exhibited oestrus, on the average, at the age of 7 months (about 5½ months retardation); and the other two failed entirely. The least stunted group showed slightly retarded puberty and less than normal regularity of the oestral cycles. In a general way, the degree of disturbance was roughly proportional to the degree of quantitative stunting of the animals.

The effects of changes in the proportions of carbohydrate, fat, and protein content of the diet vary somewhat according to the degree of deficiency of one or more of the three variables. In general, nutritive regimes involving the withdrawal of carbohydrate are not deleterious to the early appearance and regularity of the oestral cycles of the rat. With low amounts of protein (12 per cent or less) fat free diets postpone the age of pubescence and reduce the fre-

quency of oestrus. Growth, on the other hand, may be normal. Young animals reared on a diet in which the sole source of protein is that of the wheat kernel show marked stunting although adults may be maintained on this diet without injury for long periods of time (100 to 200 days). Of a group of 13 young stunted by this qualitatively deficient diet, 7 had no oestral cycles whatever during 165 days of observation (normal age of puberty is about 50 days). Of the remaining 6, three had only the initial cycle. This defect can be corrected by the addition of casein to the defective diet. Deficiencies in inorganic salts gave a definite retarding effect on the age of puberty and the regularity of the oestral cycles.

Slonaker and Card (15) reported a delay in the age of puberty in animals fed a strictly vegetable diet as compared with animals having an addition of animal protein to this strictly vegetable diet. The delay was slightly greater in the females than in the males. The menopause was hastened in the restricted group and impotency appeared in the males at an earlier age than in the group receiving the additional allowance of animal protein.

Stone (17, 18) observed that quantitative restriction of food in which the day's ration of a well balanced diet was only sufficient to hold male rats at maintenance during periods of 20 days, beginning with the ages of 20, 30, and 45 days, retarded the appearance of the initial copulatory act on the average from 16 to 23 days. Delays of smaller amounts were incurred in rats fed *ad libitum* for 20 days on corn starch (60 per cent), lard (15 per cent), casein (20 per cent), and a salt mixture (4 per cent). This diet is especially deficient in vitamins A and B.

EFFECTS OF INANITION ON LEARNING

Anderson and Smith (1) have investigated the effects of chronic inanition upon the learning ability of rats. Quantitative stunting was temporarily produced by systematic reduction of the daily ration of a well balanced diet and qualitative inanition by the use of gliadin as the sole source of nitrogen in a diet otherwise adequate. On the latter diet animals are able to maintain themselves but are not able to grow. The synthetic diet used for the control group and for quantitative stunting consisted of casein (18 per cent), cornstarch (51 per cent), lard (22 per cent), cod-liver oil (5 per cent), salt mixture and dried yeast (4 per cent). The qualitatively deficient diet differed from the foregoing only with respect to the replacement

of casein by gliadin. Two mazes of moderate difficulty were used to measure learning ability. The criteria consisted of time, errors, and excess distance in the preliminary experiment and time and errors in the main experiment.

Two groups of animals are reported for the preliminary experiment. The controls, 5 in number, were maintained on the standard diet and the experimental group, 8 animals, qualitatively stunted on the deficient (gliadin) diet. These groups were given 30 trials on the maze, 3 trials a day for 10 days, after 23 days of maintenance on their respective diets. Then followed a period of idleness lasting for 62 days after which they were again trained exactly as in the original instance. After this relearning period the stunted animals were placed upon the standard diet and for the next 60 days allowed to recoup lost weight. Their mean weight at the end of that time was almost equal to that of the controls. After realimentation they and the controls were subjected to a second relearning series duplicating that of the original and that of the first relearning series. These experiments yielded data for control and experimental groups that were essentially similar on the original learning series. On the first relearning test the experimental group had markedly lower time, error, and distance records. Essentially similar records were obtained for both on the second relearning period. No satisfactory cause for superior records of the experimental group on the first relearning series was found, hence another and more elaborate experiment was performed. In the second experiment three groups were carried forward simultaneously. At the outset these animals were trained on the maze for 30 trials, 3 trials per day. On the basis of individual time scores, three groups of equal ability were selected. Then followed a 28-day period of idleness in which the first group was maintained on the standard diet, the second group quantitatively stunted by a restricted daily allowance of the balanced diet, and the third group qualitatively stunted by being fed upon the gliadin diet. At the end of 28 days a relearning period followed in which all were given "18 trials or six days on maze I, the original maze, 12 trials or four days on maze II, which was in part similar, in part different from the first maze, then 12 trials or four days on maze I again." Thereafter the two stunted groups were fed liberally on the standard diet for 28 days to allow them to regain most of the lost weight. This was followed by a second relearning period for all groups, consisting of "12 trials or four days in maze I, 12 trials or four days in maze II,

and 6 trials or two days again in maze I." Although the two experimental techniques are somewhat different the basic results for time data are in harmony, but not those for error data. The method of selection of the three groups made practically certain that the original time curves should be identical. On the first relearning period the stunted animals gave similar records and were consistently and significantly faster than the control group. This superiority was very greatly reduced, however, in the second relearning period after the period of realimentation. The original pairing method did not equate the groups as to numbers of errors on maze I. The control and qualitatively stunted group were slightly superior to the quantitatively stunted. In the first relearning period the quantitatively stunted animals were quite consistently inferior to either of the others; the latter by turns were superior and inferior to each other. Differences between the three groups largely disappeared in the second relearning period. Concluding for the experiment as a whole it may be said that although certain aspects of the study require further investigation to clear up equivocal points, the most satisfactory explanation of the results obtained appears to hinge upon differences in motivation rather than upon fundamental differences in learning ability produced in the animals.

BIBLIOGRAPHY

1. ANDERSON, J. E., and SMITH, A. H., The Effect of Quantitative and Qualitative Stunting Upon Maze Learning in the White Rat. *J. Comp. Psychol.*, 1926, 6, 337-359.
2. EVANS, H. M., and BISHOP, K. S., On the Relations Between Fertility and Nutrition. II. The Ovulation Rhythm in the Rat on Inadequate Nutritional Regimes. *J. of Metab. Research*, 1922, 1, 335-337.
3. EVANS, H. M., and BISHOP, K. S., On the Relations Between Fertility and Nutrition. IV. The production of Sterility with Nutritional Regimes Adequate for Growth and Its Cure with Other Food-stuffs. *Ibid*, 1923, 3, 233-316.
4. GREEN, H. H., Perverted Appetites. *Physiol. Reviews*, 1925, 5, 336-348.
5. HESS, A. F., *Scurvy, Past and Present*. J. B. Lippincott Co., Philadelphia and London, 277 pp.
6. HITCHCOCK, F. A., The Effect of the Luxur Consumption of Meat Upon the Voluntary Activity and Growth of the Albino Rat. *Amer. J. Physiol.*, 1926, 79, 206-217.
7. HOLDEN, F., A Study of the Effect of Starvation Upon Behavior by Means of the Obstruction Method. *Comp. Psych. Monogr.*, 1926, 3, 1-45.
8. JACKSON, C. M., *The Effects of Inanition and Malnutrition Upon Growth and Structure*. P. Blakiston's Son and Co., Philadelphia, 1925, 616 pp.

- 8a. MARSHALL, F. H., The Internal Secretion of the Reproductive Organs. *Physiol. Reviews*, 1923, 3, 335-358.
9. MCCOLLUM, E. V., *The Newer Knowledge of Nutrition*. Second edition. The Macmillan Co., New York, 1922.
10. MENDEL, L. B., *Nutrition: the Chemistry of Life*. Yale University Press, New Haven, 1923, 150 pp.
11. MITCHELL, H. S., and MENDEL, L. B., The Choice Between Adequate and Inadequate Diet, as Made by Rats and Mice. *Amer. J. Physiol.*, 1921, 58, 211-225.
12. OSBORN, T. B., and MENDEL, L. B., The Choice Between Adequate and Inadequate Diets as Made by Rats. *J. Biol. Chem.*, 1918, 35, 19-27.
13. RICHTER, C. P., A Behavioristic Study of the Activity of the Rat. *Comp. Psychol. Monogr.*, 1922, 2, 55 pp.
14. SLONAKER, J. R., The Effect of a Strictly Vegetable Diet on the Spontaneous Activity, the Rate of Growth, and the Longevity of the Albino Rat. *Leland Stanford Junior University Publications*, 1912, 9, 1-36.
15. SLONAKER, J. R., and CARD, T. A., Effect of a Restricted Diet. II. On Pubescence and the Menopause. *Amer. J. Physiol.*, 1923, 64, 35-43.
16. SLONAKER, J. R., and CARD, T. A., The Effect of a Restricted Diet. V. On Mortality, Cannibalism and the Sex Ratio. *Amer. J. Physiol.*, 1923, 64, 297-310.
17. STONE, C. P., Delay in the Awakening of Copulatory Ability in the Male Albino Rat Incurred by Defective Diets. I. Quantitative Deficiency. *J. Comp. Psychol.*, 1924, 4, 195-224.
18. STONE, C. P., Delay in the Awakening of Copulatory Ability in the Male Albino Rat Incurred by Defective Diets. II. Qualitative Deficiency. *J. Comp. Psychol.*, 1925, 5, 177-201.

HABIT FORMATION AND HIGHER MENTAL PROCESSES IN ANIMALS

BY EDWARD CHACE TOLMAN

University of California

The present review covers primarily the year 1926, though earlier and later contributions will be referred to where the argument seems to demand it. The last review on our topic appeared in the Bulletin (36) a year ago and covered the years 1921-1925, inclusive.

The experimental literature for 1926 can be treated under two heads: I, experiments which measure with further precision the effect of relatively mechanical factors in learning; II, experiments and investigations which lead to a new nonmechanical envisagement of learning. Finally, under a third head, III, the reviewer will indulge in certain theoretical speculations.

- I. Mechanical factors: Under this head will be included:
 - A. Experiments measuring sub-mammalian learning.
 - B. Experiments dealing with the reliability and validity of maze scores.
 - C. Experiments seeking to measure the relative effects of different distributions of practice.
 - D. Experiments measuring the effects upon learning of special physiological conditions, including cerebral and cerebellar destructions.
- II. Nonmechanical factors: Under this head will be included:
 - A. Experiments investigating the "Gestalt" of perceptual fields.
 - B. Experiments leading to a new envisagement of maze learning.
 - C. Experiments concerning "insight" and "higher mental processes."
- III. Theory: Under this head the differences, if any, between trial and error learning and "insight" learning will be discussed.

I. EXPERIMENTS WHICH MEASURE WITH FURTHER PRECISION THE EFFECT OF RELATIVELY MECHANICAL FACTORS.

A. *Sub-mammalian learning.* Garth and Mitchell (8) taught a land snail (*Rumina decollata*, Linne) a simple T-maze made of glass. An electric light suspended at the entrance served as the motive; for the animals are negatively phototropic. If the snail entered the blind, it was punished by means of a heated wire. If it chose correctly, it found a dark box at the end of the true path in which it was allowed to remain for a short rest. Four to six trials were usually given in a day. Normal learning curves were obtained for both time and errors. It may be recalled in this connection that Thompson (33) was unable to teach a *water snail* a Y-maze. Is the water snail fundamentally inferior to the land snail, or was not the difference probably due to some difference in the techniques of the two experiments?

Schaller (31) taught the water beetle (*Dytiscus*) to find food at a particular place. A bit of meat was fastened upon a stick, the lower end of which projected into the water. The presence of such food and the route to it were first indicated to the beetle by trailing a brush moistened in sweetened water before him, thus finally bringing him out of the water and up the stick to the booty. After enough repetitions the animal learned to go to the stick and climb up it to the point where the meat was located, in response simply to a food signal. This food signal consisted merely in the dropping of a bit of sweetened water in front of the animal. In other words, the beetle, when he received this signal, went without further guidance to the stick, climbed up and found the food.

Schaller (31) also taught these beetles an avoidance response. He taught them, that is, not to bite at a wad of cotton which had been soaked in a salty meat solution, although they would continue to bite at one which had been soaked in a sweetened meat solution. Originally they had snapped with equal readiness at both. This discrimination avoidance was produced as a result of a training series in which the salty meat cotton was impregnated with quinine. After such a training series the beetles refused to bite at the salty cotton even though no longer impregnated with quinine.

Finally, Schaller (31) taught minnows (Ellritzen) to discriminate a food color from a nonfood color, and a food geometrical form from a nonfood geometrical form. Bits of edible meat and similar bits of meat made nonedible by impregnation with quinine were

suspended upon the tips of needles about half a centimeter above the surface of the water. These needles were also mounted about one centimeter higher up with disks presenting signal colors (or signal forms). The fish readily learned to discriminate the edible food from the nonedible food on a basis of the colors or simple geometrical forms (rectangle, star, circle, triangle) mounted above the edible (nonedible) foods. These results confirm previous findings (See previous summary (36)) as to the goodness of fish vision and the possibility of teaching them discrimination habits.

B. *Reliability and validity of mazes. Methods of scoring.* Warden (41) has examined again the data of his previous study on the "Distribution of Practice in Animal Learning" (40) to discover how his results then obtained would be affected if he had scored in terms of other norms of mastery. He compares the outcomes, using two norms of accuracy: *i.e.*, (1) counting as errors all blind entrances however slight; and (2) counting as errors only blind entrances of more than ten centimeters; and pairing each of these with three different norms of fixity: A, a norm defining learning as complete when one perfect run (in terms of the given accuracy norm) has been obtained; B, a norm defining learning as complete only when four out of five such perfect runs have been obtained; and C, a norm defining learning as complete only when nine out of ten such perfect runs have been obtained. The same general conclusions as to the effect of the different distributions of practice upon the ease of learning showed up with each of the resultant six methods of scoring though there were some minor shiftings about, and though the degree of contrast between the results for the different distributions of practice became less marked as the more rigid norms were used.

The reviewer's own reaction to the whole matter of norms is, first, to feel that as far as *fixity* is concerned the problem can best be met, not by attempting to score in terms of *trials*, but by substituting instead the procedure of running all animals the same number of trials,—this number great enough so that at the end of the experiment nearly all the animals shall have finally achieved mastery. In this way the learning curves for individual animals or groups of animals can be compared throughout their *whole* lengths. And the differences which are sought for, between individuals or between groups of individuals, can be examined at all the different stages of these learning curves. For it may be that the beginnings and ends of the curves may have different stories to tell. And if so, any attempt to

lump such differences into a single figure, such as differences between total trials, may be misleading. Secondly, the reviewer would feel that as regards *accuracy* (*i.e.*, what length of blind entrances to count as errors) further investigations directly centered on this problem are needed. Thus it may be noted that some work, done at California but not published, suggests that although partial errors (relatively slight blind entrances) correlate relatively highly with whole errors, they are nevertheless affected also by something like emotional factors which do not enter into whole errors (*i.e.*, complete blind entrances) to the same extent. But, if such be the case, then the decision as to whether to count slight blind entrances or not will depend upon what one is seeking to measure. Obviously, more work needs to be done to discover just what the interrelations between the different degrees of blind entrances are,—how nearly they do or do not measure the same thing and that the thing that one is or is not interested in investigating.

Reliability. Hunter and Randolph (14) present further evidence as to the unreliability of the maze. They used a simple T-maze with angora goats. The animals had to pass through the maze in going from their corral where they spent the night to the pasture where they spent the day (the day's ration of food and water was obtained in the pasture). Time records only were recorded. Three groups of three trials each were given. The second group of three trials was separated from the first by a rest interval of thirty days, during which the animals spent night and day in the pasture. The last group of three trials was separated from the second group by a similarly spent rest interval of 120 days. The correlations between the scores for each group of three trials correlated against the scores for each of the other two groups ranged from .065 to .316. In short, these data substantiate the earlier findings of Hunter and his students as to the unreliability of mazes.

At this point the reviewer must report, as will appear in forthcoming articles, that both Tolman and Nyswander (37), and Stone and Nyswander (32) have been able to obtain, using rats in mazes, reliability coefficients of .90 and over. And, very briefly, their results indicate that the trouble with previous mazes has been that the latter have been too short and too heterogeneously constructed.

Carr (6), in a criticism of Hunter, takes particular exception to the latter's conclusion that because mazes give low reliability coefficients, therefore the results from them are meaningless in the case

even of group differences. As Carr points out, two issues are involved: (1) the use of the maze as a measure of individual differences; and (2) its use as a measure of group differences. Hunter is right that if mazes continue to give low reliability coefficients, they must be abandoned for measuring individual differences. It does not, however, follow, as Hunter asserts, that they must also be abandoned for measuring differences between group means. As Carr points out, the usual statistical formula for the significance of a difference between group means, *i.e.*, the difference between the means divided by the sigma of this difference, contains no reference to reliability coefficients. Carr suggests, therefore, that Hunter address himself to the statisticians.

Hunter (13), in reply to Carr, reiterates in a general fashion the importance of reliable instruments. And, finally, he quotes a letter from Kelley in which the latter suggests as a practical rule that if an investigator is to work successfully on individual differences, he must use an instrument with a reliability coefficient of .90 or better; whereas if he is to work on group differences, he needs only an instrument which gives a reliability of not less than .40. Kelley does not explain the theoretical justification for this difference in the two requirements.

Tryon (38), taking this controversy between Carr and Hunter as his starting point, seeks to derive an improved statistical formula for the significance of the difference between two means, which shall contain a reference to the reliability coefficients. And this corrected formula turns out to be such that it appears that as the reliability of one's instruments goes down, any difference between two group means actually obtained (assuming, of course, large numbers) seems to become more rather than less significant. This, at first sight paradoxical, conclusion has, it would seem, none the less a certain amount of common-sense justification. For all it means is that if a difference between the means of the two groups is *actually obtained, in spite of* the unreliability of the instruments, the chances are greater that there was a true difference behind and producing this obtained difference. For the unreliability of the instruments would, as such, tend to obscure any such true difference and to reduce the probability of an obtained difference being found.

Finally, whether or not this new formula of Tryon's proves able to withstand critical attack, it seems to the reviewer at any rate obvious that work with group differences does not require as reliable

instruments as does work with individual differences (Kelley also indicated this in his letter quoted by Hunter). For if the groups worked with are large enough and if a real difference between their respective true means does exist, the latter will in time (*i.e.*, after the measurement of enough cases) be bound to manifest itself, even though each individual measurement be relatively unreliable. (For an amplification of this argument, see the article by Tolman and Nyswander (37) already referred to.) The real criticism, as the reviewer sees it, to be directed against most of the conclusions drawn from work with animal mazes in the past lies not in the unreliability of the mazes used but in the smallness of the numbers of animals that were run. The groups run have usually been so small in number that no statistical criteria of any sort could properly be applied to them.

C. Different distributions of practice. Williams (44) tested some seven dogs (five cocker spaniels and two Scotch terriers) in three successive discrimination experiments: *i.e.*, (1) the choice of the duller of two five-centimeter circles; (2) the choice of a flickering as against a steady light; (3) the choice of a steady as contrasted with an intermittent buzzer. After the given discrimination had been practiced to a given standard of perfection, a ninety-day rest interval intervened and a retention (relearning) test was given. Then the next type of discrimination and its retention were tested. Three different arrangements of practice were distributed among the three different problems and the seven different animals. These arrangements of practice were as follows: A, 5 trials 4 times a day, 4 hours apart; B, 10 trials twice a day, 10 hours apart; C, 20 trials once a day. (In the relearnings the repetitions were consecutive.) *As to original learning*, the greater the distribution of practice, the more repetitions were required for the original mastery. *As to retention*, it appeared that the greater the distribution of practice, and hence the greater the number of repetitions in the original learning, the greater the retention.

Williams also examined different distributions of practice in maze learning. His dogs learned eight successive mazes, and again three different arrangements of practice were distributed among these different problems and the different animals. Arrangement A consisted in 3 trials 4 times a day; arrangement B in 6 trials twice a day; and arrangement C in 12 trials once a day. No retention tests were given. Here the greater the distribution of practice, the sooner the original learning.

In evaluating both these sets of results, it must be noted that the number of animals was so small and the interacting effect of practice of one problem upon the next so uncontrolled that the findings can be taken as suggestive only. At their face value, however, they seem to indicate that distributed practice is more favorable for original learning in the case of maze experiments, but less favorable in the case of the discrimination experiments. This greater length of time spent in the original learning in the case of the discrimination experiments seems to be compensated for, however, by better retention. Whether or not this difference as regards the effects of distributed practice upon the original learning of discrimination problems and of maze problems suggests a fundamental difference between these two types of learning is a point wanting further investigation.

D. Special physiological conditions. Ball (3) investigated the influence of the oestrus cycle in white rats upon maze learning. The females were examined by the smear method. She ran an experimental group (16 animals), one trial each oestrus (that is, one trial approximately every four days), and a control group (16 animals) one trial also approximately every four days, but during dioestrus. No significant differences appeared between the two groups. She concludes that, at least when food is used as the incentive, the female sex cycle does not influence maze learning.

Anderson and Smith (2) contrasted the abilities of stunted rats and control rats of the same age and previous training to relearn a maze and to learn a new maze. Two methods of stunting were used: (1) a qualitative method in which the animals were fed the usual weight of food but in which gliadin was substituted for casein as the protein in a "normal" diet; (2) a quantitative method in which the complete normal diet was fed but in lesser amounts. Results: (1) the qualitatively stunted animals, while stunted, made uniformly better time and better error records than the controls; (2) the quantitatively stunted animals, while stunted, made better time records but somewhat worse error records than the controls. When realimentation was established, both groups again approximated the control group in both time and errors. The authors suggest two possible explanations: one, that stunting produces its general tendency to enhance learning primarily through increasing the drive; the other that it, as such, retards physiological age, and that it has already been demonstrated that younger animals learn somewhat faster than older ones. In this connection the reviewer would like to suggest that such find-

ings as there may be on age differences are also, he believes, to be interpreted in terms of drive, that is, that the younger animals, as such, have a greater hunger and therefore a greater motive for running the maze than do the older animals.

Lashley (19) and Lashley and McCarthy (20) have during the year added two more contributions to the now extensive list of Lashley's investigations upon brain function in learning. The first of these constitutes the seventh in his series entitled "Studies of cerebral function in learning." It was summarized in our BULLETIN review of last year (36). The nature of the investigation it reports is indicated by the specific title, "The relation between cerebral mass, learning and retention." The procedure of the experiment consisted in destroying varying amounts of the occipital region in different rats and then training them in the visual discrimination habit. It was found that the ease of the original learning was unaffected by the amount of the occipital region destroyed before the beginning of the learning. On the other hand, when the occipital lesions were made after the habit had been acquired, a very high correlation was found between the amount of the destruction of the region and the resultant loss of the habit as measured by a retention test. This correlation between extent of lesion and loss of habit was .70 plus. There was no relationship found, however, between the specific part of the region destroyed and the loss of the habit. The general conclusion arrived at as a result of this and the preceding experiments in the series may be summed up in Lashley's own words: "No part of the cerebral cortex is better adapted for the formation of any particular habit than is any other. Any anatomically continuous cerebral area may serve the learning function, provided it presents a sufficient mass. This must mean that in a problem situation the effects of stimulation irradiate to all parts of the cortex. As the habit is established there comes into being a definite structural modification having topographical position and capable of destruction by brain injury. The learning process is independent of locus, whereas the mnemonic process or engram has a definite localization."

The second paper for the year, that of Lashley and McCarthy (20), investigates the survival of the maze habit after cerebellar injuries. Seven rats were taught a rectangular maze with eight *culs-de-sac* and later given a retention test. Then the cerebellum of each rat was more or less completely destroyed by cauterization through a median trephine opening just back of the parieto-

occipital suture. A second retention test was then given. There was practically no loss of the habit save in the case of one animal. In the case of this animal there proved, however, to have been a widespread infection which prevented any clear interpretation of this loss of the habit. It is noteworthy, however, that this animal relearned the maze with perfect success, although the postmortem showed that his cerebellum had been completely destroyed. In the case of two rats the cerebellar lesion was preceded by enucleation of the eyes. These animals also retained the habit successfully. This last proves, the authors think, that these animals did not need to fall back upon exteroceptive cues but were continuing to react on the basis either of kinesthetic stimuli or of some centrally organized mechanism. (They feel that the maze itself was constructed and controlled so as to offer no differentiating olfactory and tactile stimuli.) Their final conclusion is that the cerebellum plays no part in the learning or the retention of the maze habit.

One may here briefly summarize and evaluate all these contributions under this first heading of mechanical factors. The reviewer would schematize them as follows:

A. Further evidence that sub-mammals (fish and waterbeetles) are capable of acquiring both discrimination and food position habits.

B. Relatively unreliable mazes can be used to measure group differences provided the groups are large enough. Properly constructed difficult mazes will give high reliabilities even with rats. (At the date of the present writing, the articles in support of this latter finding have not yet appeared, but are about to appear.)

C. Further conflicting evidence on the relative advantages of distributed and of concentrated practice. Some suggestion that maze habits and sensory discrimination habits behave differently in this matter. Evidence that longer learning time induced by more distributed practice makes for better retention.

D. The female sex-cycle seems to have no effect upon maze learning.

The cerebellum is not involved in the maze habit.

And as regards the cerebrum: "No part of the cerebral cortex is better adapted [save for the closeness of its anatomical connections to the given incoming and outgoing paths] for the formation of any particular habit than is any other. . . . This must mean that in a problem situation the effects of stimulation irradiate to all parts of the cortex. As the habit is established there comes into being a

definite structural modification having topographical position and capable of destruction by brain injury. The learning process is independent of locus, whereas the mnemonic process or engram has a definite localization."

So much for these already accepted, relatively mechanical factors. No particularly new envisagement as to the nature of learning has arisen out of them.¹

II. EXPERIMENTS AND INVESTIGATIONS WHICH LEAD TO NEW NONMECHANICAL ENVISAGEMENTS OF LEARNING

A. *The "Gestalt" of the perceptual field.* Under this one head we shall group together three types of experiments as follows: (1) Experiments proving that animals (hens) respond to object qualities rather than to mere sensation qualities. (2) Experiments investigating "abstraction," *i.e.*, the tendency, after animals have been taught to discriminate two objects differing both as to color and as to form, later to discriminate in transfer experiments according to the previous form, or according to the previous color (hens, fish). (3) Experiments investigating the perceptual cues involved in "homing" (bees, ants, wasps, pigeons).

(1) *Object-qualities.* Gotz (9), under carefully controlled conditions, trained hens first to choose the larger of two grains of corn, when both grains were at approximately the same distance at the moment of choice. He then placed the larger grain at a sufficiently greater distance from the choice point so as to cast a retinal image only one-thirtieth of that cast by the smaller grain. The hens still chose the actually larger grain. This "Sehgrößenkonstanz" maintained itself even through variations of perspective foreshortening due to turning the grains at different angles relative to the vision of the oncoming bird.

(2) *"Abstraction" experiments.* Schaller (31), in addition, as reported above, to teaching his minnows (Ellritzen) to distinguish a

¹ This does not hold, perhaps, for some of Lashley's work, particularly some of the experiments reported in the review a year ago. Those results indicated that the *simple* reflex arc concept of habit is no longer tenable. Thus a rat who had learned with only his right eye could then perform the habit without further practice equally well with only his left eye. And a monkey who had learned to open a box with his right arm, his left arm being at the time paralyzed due to cerebral lesions, could later without further practice, when this right arm had itself become paralyzed, perform the habit with his left arm, which in the meantime had recovered.

food color from a nonfood color and a food form from a nonfood form, also investigated the relative dominance of color or of form when the cues presented differed in both. Thus, after he had first taught the fish to discriminate two cues which differed both as to color and as to form, he then transferred the animals to a new pair of cues in which the connections between color and form were reversed. Presented with this new pair of cues, one fish responded according to the previous color contrast, the other fish according to the previous form contrast. It appeared, however, that if the two original cues differed outstandingly in color, then both fishes tended to respond to color in the second arrangement; while if the original cues had differed outstandingly as to form, both fish responded to form in the second arrangement.

Kroh and Scholl (18) made a similar investigation of the relative dominance of form and of color in hens. The birds were taught to pick from blue circles but not from red triangles. They were then presented with red circles and blue triangles, with the result that they then picked from the blue triangles, thus proving the dominance of color. A control test was instituted in which the birds were presented with circles and triangles both white. They picked with equal readiness from either. That is, no influence of form whatever held over from the original training. They were next, however, trained successfully to choose the white circles as against the white triangles; thus showing that the birds could discriminate according to form when necessary. The authors compared their results with those of previous investigators (*e.g.*, Révész, 30) and suggest that all such experiments should properly be designated investigations of "Teilinhaltlicher Beachtung" (discriminative response to partial contents) rather than investigations of "abstraction." The latter term should be reserved for cases involving higher conceptual processes. This recommendation seems sensible.

(3) *Perceptual cues in homing.* Rabaud presents certain new experiments (28) and an extremely important and thoroughgoing theoretical analysis based upon all the experimental data to date (29) concerning the perceptual cues to be assumed in the explanation of the homing instincts of insects (wasps, bees, ants) and of pigeons. A really adequate summary of the argument is possible in a short space. The author divides the process of homing into three parts: (a) the going in the correct direction to the immediate general locality of the nest; (b) the recognition of this locality; and (c) the

recognition of the nest itself. The general conclusion seems to be that the great majority of the evidence indicates as regards (a) that the animals in finding their way back to the general location of the nest use ordinary perceptual cues either of vision or of olfaction, primarily the former in the case of bees, wasps, pigeons, and primarily the latter in the case of ants. (Though it appears that if the usual cues fail, others can be resorted to.) As regards (b) and (c), the recognition of the general locality of the nest and the recognition of the nest itself, it appears that the two processes are intermingled. In other words, the nest does not seem to be singled out and recognized, as such, but rather it sinks into the other features immediately surrounding it. Thus if the nest be moved to one side during the absence of the animal, the latter upon returning is apparently guided by the general complex of stimuli coming from various adjacent environmental features and is led by them to try to find the opening of the nest at the old place. In other words, to talk in Gestalt terms, the "figure" which stands out for these animals seems to be not the nest, as such, standing out as it would for us upon the "ground" of the other surroundings, but rather the "figure" which stands out is apparently a complex uniting within itself both nest and surroundings. The nest is not an object independent of its immediate environment, but rather it and the immediate environment make a single object. Rabaud's article contains an important bibliography of seventy-one titles.

Summing up under the "Gestalt" of the perceptual field, it would appear: (1) that animals normally tend to react to object-qualities, *i.e.*, to qualities which maintain their constant size-, and shape-, and quality-values, rather than to momentary sense-qualities *per se*; (2) that when forced to discriminate between two objects differing in both color and form they tend to react to one of these, the one most striking under the given circumstances; and (3) that in finding and recognizing locations (as in homing) they are not rigidly bound to stimuli coming from any one sense mode.

Finally, it ought to be pointed out that this matter of the "Gestalt" of the perceptual field is an important item for the understanding of learning since the way a given animal is or is not able to "gestalt" his field will set the limits within which his learning, whether of the trial and error or the insight variety, can take place. The learning of animals is not, it would seem, a simple mechanical affair of unit stimuli and unit association bonds, but is rather a

process arising out of and always statable in terms of meaning. Indeed, according to the Gestalt psychologists (see Koffka, 16, 17, in particular), learning is to be described primarily as merely a "re-Gestaltting," often of a simple perceptual order, going on within the phenomenal field. (See also Hempelmann's recent and important book on animal psychology, 10, p. 509, for an endorsement of this general Gestalt point of view.)

Let us turn, now, to the new experiments which, it seems to the reviewer, emphasize and reinforce the necessity of some sort of meaning concepts for the description of learning.

B. *New envisagements of maze learning.* Washburn (42) tested twenty white mice in a Watson circular maze and at the same time measured the strengths of their daily hunger drives. This latter she did by measuring the time spent at the end of each run actually eating (or, rather, drinking) in the food box. The animals had dried bread in their living cages continuously, but obtained their day's ration of liquid (*i.e.*, milk) in the food compartment only. They were allowed to drink as much as they wanted and the actual time spent in such drinking recorded. She also measured the actual speed of running by noting the time spent in actual movements, and also by tracing the total distances traveled. Her *first finding* is that in the case of some animals there was a high daily correlation between degree of hunger, as measured by length of time spent in lapping milk, and corresponding speed of running, while in the case of other animals there is little or no such correlation. She designates the group of animals for which there is such correlation as "hunger-driven" and the others as "activity-driven." Her *second finding* is that in the case of the hunger-driven animals there was also a high correlation between daily degree of hunger and goodness of error score on that day, while for the activity-driven animals such correlations were low. Her *third finding* is that as between individual mice there was no correlation between total learning ability and the degree to which the animal tends to be hunger-driven. In other words, in spite of the fact that one might expect hunger-driven animals to be, as such, better learners than activity-driven animals, such differences, if operative, were at any rate not sufficient to obscure the greater innate differences due to differences in "general ability" or "I.Q."

To the reviewer's mind, this experiment of Miss Washburn's, though only a beginning, is most important. It brings to a sharp

focus, in a way that has not been done before, the fact that our animals run mazes for divergent motives. And may it not turn out that some of the differences as to methods and kinds of learning, which have been obtained, may eventually be traceable to such differences of motive? To suggest an example: it will be remembered that whereas Peterson (27) found that short blinds are eliminated first, White and Tolman (43) found that long blinds are eliminated first. May it not be that such a difference might be due to differences in the degrees of hunger under which the two sets of rats were run? It might be that activity-driven rats would *prefer* long blinds, "as something capable of much exploration," whereas hunger-driven rats would, rather, *dislike* long blinds "as causing undue delay in reaching the food." If so, then if Peterson's rats were less hungry than White and Tolman's, we should expect the contrast between results which was actually obtained. Such a possibility is not, perhaps, to be taken particularly seriously. It is merely thrown out by the reviewer as an illustration of the kinds of possibility which, in his mind, Miss Washburn's findings open up.

Alonzo (1) has added another investigation to the problem of the effect of guidance upon maze learning. His animals were taught a relatively simple right-left maze and guided through it for a certain number of trials by means of a leash attached to a collar about the neck of the animal. He compared ten different groups as follows: group 1, no guided trials; group 2, trials 1 and 2 guided; group 3, trials 1 to 4; group 4, trials 1 to 6; group 5, trials 1 to 8; group 6, trials 1 to 12; group 7, trials 1 to 16; group 8, trials 1 to 20; group 9, trials 3 to 6; and group 10, trials 5 to 8. In general, guidance was effective; that is, the animals which had had a certain number of guided trials usually required considerably less subsequent unguided trials than did those animals which had had no guided trials. (An exception appeared in the case of group 2, for which the first two trials were guided. These animals required more subsequent unguided trials than did those which had had no guided trials whatsoever. This result may have been a statistical fluke since there were only 16 rats in each group.) It appeared, secondly, however, that the guided trials, although teaching something, did not teach as much as a corresponding number of unguided trials. Thirdly, it appeared that guidance introduced after some initial nonguidance trials, *i.e.*, groups 9 and 10, produced the most effective arrangement of all. The animals in these latter two groups learned with a smaller number

of total trials (guided and unguided) than did any other group, including the group with no guided trials at all. Finally, it may be noted that a few animals in nearly every group succeeded in mastering the maze during the period of guidance alone. That is, it is possible for a maze to be learned without any *actual* entrances into the blinds. This last seems to be the author's most significant conclusion.

He compares this last result with the previous ones of Koch (15), Ludgate (24), and Wang (39). Ludgate used a somewhat similar method with stylus mazes and human beings. During the guided trials she directed the subject's hand by taking hold of it. Her results differ from those of Alonzo in that her subjects were never able completely to learn the maze by guidance alone. This difference Alonzo attributes, and it seems to the reviewer rightly, to the fact that Ludgate's human subjects behaved in a different manner from that of the rats during guidance; the human subjects were relatively passive and did not, during guidance, note blinds or attempt to enter them. The rats, on the other hand, strained at the leash and made active attempts at going into the blinds. Hence Ludgate's subjects had no chance to learn about the blinds during guidance and to eliminate them, whereas Alonzo's subjects did have such a chance.

Koch performed an experiment on guidance, using both animals and humans. Instead, however, of a leash or similar control, the blind alleys were blocked during the period of guidance. Her results also differ from Alonzo's in that for her also none of the subjects, animal or human, were able completely to learn the maze during the guidance period alone. Alonzo points out that with Koch's subjects also there were no tendencies to make errors during the guided trials, and hence no opportunity offered for their correction and elimination.

Finally, Wang used a method of verbal guidance with human beings, in which the subjects were corrected verbally whenever they started to make an error. Wang's results agree with Alonzo's in that his subjects were on occasion able to master the maze completely during the guided trials.

Alonzo's conclusion is that in order to obtain complete and final blind elimination it is necessary that during the learning either actual entrances or attempts at entrances must be made. Otherwise such errors never have a chance to be completely corrected. Or as Carr (5) puts it: "A certain number of errors must be made and eliminated before the subject is ever able to run the maze correctly.

Correct modes of response are established in part by *learning what not to do*.² Undoubtedly the fixation of the correct response is partly responsible for the elimination of errors, but it is equally true that the establishment of the correct mode of response is an incidental result of the eliminative process." Or, to put it in his own words, the reviewer would conclude that learning, even in the case of a maze, must be said to be a process exhibiting the earmarks of insight. For the type of practice which most favors learning is the type which emphasizes the wrongness of the wrong as well as, and in contrast to, the rightness of the right.

Higginson (12) sets out to see if the rat, like the ape, is capable of "an extension of visual apprehension such as to initiate a sudden shift in the actual performance which is incapable of explanation by the usual conception of 'trial and error' and by the 'laws of frequency and recency.' Can the rat visually perceive to advantage a sudden change in its path which offers a major reduction in its usual course towards food?" He used a standard circular maze and at the entrance to alley 3 he put a snugly fitting door. During the first hundred trials the rat on coming down alley 2 finds this door closed, that is, he finds a smooth wall at his right, and he is required to run to the end of the *cul-de-sac* at his left. Only upon returning from this *cul-de-sac* does he then find the door into alley 3 open. In other words, during these hundred trials the rat develops a habit of running six feet out of his way down the *cul-de-sac* and back again. After these hundred trials the door is then opened and left open for all subsequent trials. Curiously enough, when the change was made only four of the nine rats ran into the blind and out again before turning into the newly opened door, and these four immediately shifted. And what is more significant, the remaining five "stopped suddenly and without interference ran the remainder of the maze correctly, thus dropping *at once*³ six feet from the previous pathway and turning in a different manner." These results, as Higginson insists, are "inexplicable in the usual categories of 'kinaesthetic patterns' and 'frequency and recency' of problems." He concludes that, given the particular demand made upon his animals, "visual perception constitutes under the conditions an important functional resource for the organism." The reviewer is heartily in agreement with the probable correctness of this conclusion. It does, however,

² Italics mine.

³ Italics mine.

seem to him that there is a possible source of error in Higginson's experiment in that there seems (as has been found in the California laboratory) to be a general tendency for rats to enter *any newly opened pathway*. And in so far as this is true, the sudden switch from going down the useless *cul-de-sac* to leaving it out and going directly into the newly opened door may have been merely the expression of such a general tendency to enter new pathways, and not an "insightful" apprehension of the shorter distance as such.

Summing up these experiments of Washburn, Alonzo, and Higginson, they, it seems to the reviewer, agree in suggesting: (1) that maze learning takes place only under the spur of a motive or end; (2) that it is sensitive to changes in the nature of that end; and (3) that it must be described as of the nature of an improved knowledge of, insight(?) into, the position of that end.

We turn now, finally, to insight experiments proper.

C. "*Insight*" and "*higher mental processes*." Nelimann and Trendelenburg (25) repeated many of Köhler's "Umweg" experiments with monkeys, a *Rhesus* and a Pavian (*P. cynoceph*), both newly imported at the time the experiments began. They carried out some eighteen experiments. (Most of the successes reported, however, were obtained from the *Rhesus*.)

(i) Reaching experiments. These investigated the monkey's ability to estimate correctly the distance of food. Food was placed outside the cage, sometimes within reaching distance and sometimes beyond it. It was found that the monkey estimated very accurately (*i.e.*, to within two or three centimeters) whether or not he could reach the food with naked paw. If it was just out of reach, he did not attempt to grab for it.

(ii) String experiments. The monkey discriminated readily between a string attached to or touching the food and one not touching the food. Further, if the animal was allowed to observe the placing of the string, he could differentiate between the case where he saw the string merely laid on the food and the one in which he saw it actually tied to the food. In the former case he would not pull the string; in the latter he would.

(iii) Rake experiments. The results substantiated those of other observers that monkeys will not use a rake correctly unless it has already been properly placed with teeth behind the food.

(iv) Casket experiments. A box with a hinged upper lid was used. This lid on the outside showed no difference between the edge

which lifted up and the edge which was hinged. If the food was placed in this box while the monkey was watching, and then the box was pushed to the edge of the cage with either side toward the animal, the latter never fumbled but immediately lifted the proper edge of the box, whether in placing it before the cage it had been turned through 90 degrees, 180 degrees, or 360 degrees from its original position. This memory of the box's position could not, however, be retained correctly for an interval of more than half a minute: after a longer time the monkey would forget which edge of the lid was the one toward him. In this connection it should be noted that recent experiments by Tinklepaugh (34) indicate that monkeys can delay successfully up to some twenty-four hours when the feature to be remembered is which one of two containers, relatively separated in space, the food was placed in; a striking difference, whatever the explanation may be, from the short delays obtained by Nelimann and Trendelenburg.

(v) The bolt experiment. The lid of the casket containing the food was fastened by means of bolts. These had to be pulled toward the monkey before the lid could be opened. The animal was unable to learn to manipulate these bolts except by trial and error.

(vi) Estimation of distance experiments. Fruit was hung from the top of the cage with varying lengths of suspending cord. The animals chose with great nicety the easier route for obtaining it. If it hung low enough, they reached it by a spring from the floor. If it hung higher, they made no attempt to spring from the floor, but immediately climbed to the top of the cage and reached down for it.

(vii) Swinging door experiment. The Rhesus used the top of a door to swing out on to reach suspended food immediately and without tuition.

(viii) Obstruction experiment. In the case where a box was placed against the bars of the cage in such a way as to prevent the reaching through the bars with the paw in order to obtain the food outside, the box was pushed out of the way immediately and without tuition. (A type of solution not achieved by Köhler's apes.)

(ix) Experiments involving angles and distances. When the further end of a string was tied to a point at some distance from the cage and fruit tied at a point on the string nearer the cage and then the string brought into the cage in an oblique direction, the animal readily and without trial and error moved the string hand

over hand until it came perpendicularly to the cage, and thus brought the food within reaching distance. A similar solution was achieved when a stick was substituted for the string. In the case of the stick the pivot point of the stick was immediately adjacent to the cage and the fruit was placed at a point beyond the pivot. The stick was immediately turned into a position parallel with the cage and the fruit thus brought within reach.

(x) Pendulum experiment. When the fruit was swung on the end of a string pendulum, the monkey immediately took his stand at the proper position on the side of the cage for catching the fruit at the end of one of its swings.

(xi) Inverted flower pot experiment. Food was placed under one of two flower pots and then these were rotated about one another before the eyes of the monkey. After the rotation the monkey, who had been watching the process, immediately chose the right pot. He did not show "astonishment" in another experiment when upon lifting up the pot he found another one underneath, although he had not seen this latter one put in place. In other words, Buytendijk's (4) finding reported last year was not confirmed.

(xii) Turntable experiment. The food was placed upon the far side of a small turntable just outside the bars of the cage. The animal at once and without hesitation began rotating the turntable in such a way as to bring the food directly to the front of the cage.

(xiii) Mirror experiments. The monkeys when presented with a mirror sniffed at and touched their own images with much interest and responded in the usually reported fashion of peeking behind the mirror to hunt for the "other monkey."

(xiv) The hanging string experiment. When fruit was put in a high basket so that it then disappeared from the sight of the monkey, but with a string hanging from it, the latter was immediately pulled.

(xv) Tube and plunger experiment. The monkeys did not succeed in pushing food out of a hollow tube by means of a stick. Both glass tubes and opaque metal tubes were used and the stick was placed in position before the beginning of the experiment. In every case the monkey either neglected the stick or pulled it out instead of pushing it in.

(xvi) Slide ring experiment. After trying many other possibilities the monkey exhibited the solution of pulling a sliding ring to which food was attached over a slip wire to the side of the cage. He did this by means of a string dangling from the sliding ring.

(xvii) Swing rope experiment. The monkeys readily used a rope to swing on to reach distant hanging food.

(xviii) Box placing experiments. The experimenters never obtained complete success in this experiment. (The monkey died before the conclusion of the experiment.) Several approximations to success, however, did appear. The monkey spontaneously used the shoulder of an attendant to climb on and when later the attendant stood at some distance from the food, the animal pulled at his coat in a pleading fashion. The monkey also used spontaneously a loose blind to swing out on to reach the food. He also exhibited on numerous occasions a tendency to move the box a slight distance in the proper direction for getting it under the food, but invariably abandoned these attempts before the box had been moved a sufficient amount. The animal also learned readily to turn the box from lying supported at an angle to a vertical position so as to bring it into a position in which he could then stand upon it and reach the food.

In contrasting their results with those of Köhler on the apes, the authors conclude: that (1) the monkeys are far behind the apes in the use of tools; but that (2) they are apparently equal to the apes in their apprehension of spatial relationships and of spatial Umwege (*e.g.*, string, swinging rope, hindering box, etc.). And, finally, (3) they call attention to the fact that they have presented some new experiments not yet tried out with apes, to wit, the turntable, the slide ring, the hanging string.

Hertz (11) reports observations on a carrion crow (*Corvus corone*) and a jackdaw (*Coloeus monedula*), both taken as young birds from the nest and raised in captivity. They were kept in adjacent flying cages which were large enough to be entered by the experimenter. The crow was generally the quicker learner and the more intelligent of the two. Both birds were highly accurate in visual discrimination and highly sensitive to any changes in their *visual* environment, whether near at hand or at a distance. They became very friendly with the experimenter. The crow showed an amusing discrimination between the experimenter's right hand which fed him, and cared for him in general, and the experimenter's left hand which was used to hold him or restrain him. The former was treated as a friend, the latter was pecked at and attacked whenever possible.

As regards insight and higher mental processes, the following is a somewhat telescoped summary of the experimenter's observations:

(1) The crow learned to throw hard food into the water to soften it. (This seemed to arise out of an original play tendency to throw all easily moveable objects into water.)

(2) The crow exhibited considerable skill in placing food into a crevice as a holder when he wanted to tear the food apart.

(3) The crow learned to push pine nuts through the wire to the experimenter for the latter to crack open. He would even go and find hidden nuts (oftentimes seeming to recall the exact spot where he had previously hidden them) in order then to hand them out to the experimenter.

(4) The crow was less and less ready in this experiment to hand out nuts to the experimenter the more they had, by painting or other artificial means, been made to differ in appearance from normal nuts. He in play often made collections, putting nuts with nuts, stones with stones, etc.

(5) When the experimenter wished to set the bird to hunting for hidden or buried nuts, she had merely to toss a nutshell into the cage (as a symbol?).

(6) The birds would hide food and playthings in corners, in holes, etc., and cover them up with all available light objects (*e.g.*, dry leaves, loose earth, etc.), and they would uncover them afterwards, going directly to the hidden caches. As much as five hours intervened on occasion between the hiding of an object and its later uncovering.

(7) They showed insight in their methods of removing various types of obstacles that on occasion covered the food. Thus, if these obstacles proved too heavy to be dislodged by the usual direct method of inserting the bill towards the food and pushing, the bird would at times take the roundabout route of going to the side *away from* the food and from there pulling.

(8) They exhibited a capacity for delayed reaction both in the uncovering of food which they themselves had buried and in the uncovering of food which they had seen the experimenter bury or cover. (No test of the lengths of time possible were made in this latter case.)

(9) They learned, at first through accident, how to open the doors of small nest cages used as puzzle boxes. After they had once learned this, they showed considerable insight into the manner by which the doors worked. Thus the crow removed a stone which blocked the door in an insightful fashion, and the jackdaw dis-

mounted and opened the door wider from the floor in order then to mount it again and perch in a more comfortable position.

(10) The crow learned to operate a bolt that was used to lock the doors and acquired considerable insight when the position of this bolt was changed and when the door was hinged on the opposite side.

(11) Both birds showed a high mastery of all sorts of spatial "Umwege."

(12) They readily solved the pendulum experiment in which the food was swung on the end of a string and the bird had to take up the appropriate position for catching it at the end of a swing.

(13) They hauled up food put in a pocket at the end of a dangling strip of cloth. They did not attempt, however, to thus haul up the food when it was tied to the end of a string. The strip of cloth was an easier problem because they could stand on it and thus hold the part of the cloth already hauled up. This would have been impossible in the case of the string. The jackdaw, strangely enough, showed, generally speaking, more ability and insight in the case of this one test than did the crow.

Let us now compare the results for birds and monkeys. The outstanding conclusion would seem to be that the two types of animal are on much the same level as to insight. Both are very expert in visual discrimination and in spatial Umwege. And, surprisingly enough, the hands of the monkey do not seem to put him into a very greatly favored position with respect to the bird. Only in the pulling of string and such beginnings of tool-using does the possession of hands seem to give him some advantage. In all matters of spatial Umwege and of the simple moving or carrying of objects the bird is as good as the monkey.

Finally, under this head of insight let us note that Duncker (7), Lindemann (21), Lipmann (22), Lipmann and Bogen (23), and Peisers (26) have sought to try Köhler's types of insight problems with human beings, for the most part children, normal or defective.⁴

Lipmann and Bogen, and Lindemann reiterate Köhler's distinction between ability to respond to the mere optics of the situation and the ability to respond to its fundamental "static" or physical principles. Lindemann finds that his feeble-minded (imbecile) children were able, like the apes, to respond successfully to situations involving primarily

⁴ The dates of all these investigations, save Duncker's, are before 1926, but since they were not included in last year's review, I am reporting them now.

optics, but tended to fail in situations where more strictly physical, statical, principles were involved. He found, for example, in one of his defective children a similar response to that of Sultan. When the child was presented with the double stick, he pushed the one part out towards the goal with the other part, thus establishing an optically successful though physically unsuccessful connection. Lipmann and Bogen found, on the other hand, that normal children of ten to fourteen years were capable of successful solutions in cases involving physical and statical, as well as optical, principles. Duncker found that the moment of insight was a moment of "penetration" in which the subject sees what is wrong with the results of some trial (or error) which he has already tried or thought of trying. Lipmann, and Lipmann and Bogen make a distinction between the behavioristic sort of intelligence involved in problems of these sorts (*i.e.*, a knowledge of "Naive Physik") and pure theoretical or "gnostic" intelligence.

In general, these authorities all agree in envisaging insightful problem-solving as something fundamentally different from trial and error problem-solving. Here, it seems to the reviewer, is an important issue, and the remaining section of the paper will be devoted to a discussion of it.

III. THEORETICAL DISCUSSION (INSIGHT VS. TRIAL AND ERROR)

As an introduction we may note the new terminology suggested by Nelimann and Trendelenburg (25). They propose the terms "primary solution" and "secondary solution." A primary solution is one which arises when the specific problem has never been met with by the animal in his wild state, and when also it is now solved without the aid of overt "imitation," "trial and error," or "being put through." A secondary solution is, in contrast, one which does involve imitation, trial and error, or being put through. One further point about the primary solution must also be noted. Nelimann and Trendelenburg themselves do not stress this, but it seems to the reviewer obvious that in the case of a primary solution there must be supposed to have to occur, if not overt trial and error, some sort of internal happening then and there. Otherwise there would be no guarantee that the case was one of a SOLUTION at all and not merely one for which innate endowment or past habit had already prepared the appropriate response. To sum up, primary solutions do, then, set themselves off from secondary solutions chiefly in that

whereas in the latter the required new adjustments come only after, and as a result of, overt behavior, in the former they seem to come without overt behavior but rather by means of some sort of internal happening then and there.

The reviewer has previously (35, 36) indicated that he believes that both trial and error learning and "insight" learning, so-called, are to be described as passings from one set of meanings (postulations as to the position of the goal) to a second improved set of meanings (postulations as to goal position). Both the end-states of learning are, in short, to be described as states of "insight." And this we would hold to be as true for trial and error learning as for "insight" learning.

Let us elaborate this hypothesis further. And let us begin with trial and error. We may take as our example Thorndike's kitten and its learning to pull the hanging loop of string in order to get out of the puzzle box. Before the learning, the kitten has, we would say, a postulation (insight) as to the position of the goal which finds expression in the specific character and direction of the array of strugglings, *i.e.*, the bitings, scratchings, squeezings, etc., which the animal is then and there peculiarly ready for. And after the learning, he has a new improved postulation (insight) as to the position of the food which expresses itself in the now acquired, especially strong propensity for pulling at anything like a hanging loop of string. The initial array of ready behaviors defines one postulation (insight); the acquired readiness for string-pulling defines a new, improved postulation (insight). The initial array could be shown experimentally to be contingent upon the general fact of the food being outside. And hence, we shall declare, it can be said to postulate this outsideness. And the new, especially strong readiness for the string-pulling could similarly be shown experimentally to be contingent upon the sequence: pulled string—opening a way out; and hence can be said to postulate that sequence. (It may be noted in passing that this final postulation [insight] in the case of the cat does not include, apparently, any reference to the exact nature of the mechanism, whether pulley, electrical connection, or what not, whereby this sequence is achieved. The cat's readiness to pull would not, in short, prove in any way experimentally contingent upon changes in that mechanism. The animal's final postulation would be merely that of the gross fact of the physical sequence.)

Turn, now, to "insight" learning. And let us take as our example

the case of Köhler's ape and the occasion when he first used a stick to rake in the distant food. This case also would be described as the passage from one initial postulation of (insight into) the position of the food, to a second improved postulation of (insight into) that position. Before the solution, the ape's postulation would express itself in the general readiness for reaching, plus possibly some simultaneous tendency probably to suppress this readiness; this latter suppression being correlated with the excessive distance of the food. After the solution, his improved postulation (insight) would express itself by the newly acquired, peculiar readiness for the use of a stick or of any other similarly functioning long object. The initial set of reaching readinesses could, we believe, be shown experimentally to be contingent upon the actual position-relation of the food, as outside the cage and at a considerable distance, and hence to postulate this outsideness and this distance. And, similarly, the newly acquired readiness for the use of the stick, or of any stick-like object, which appears after learning, could, we believe, be shown experimentally to be contingent upon the further physical actualities (*i.e.*, the smallness and rollability of the food, etc.) whereby the distant food can, in fact, be raked in. And hence, we must say, this acquired stick readiness expresses this further insight into (postulation of) those further physical actualities.

In short, the learnings of both cat and ape are to be described as passings from one initial set of position postulations (insights) to a second improved set of position postulations (insights). But what, then, is the difference between the two cases? Let us return to the point we made above that primary or insight solutions are ones in which the new adjustments (new postulations of position) come *without* overt behavior, whereas secondary or trial and error solutions are ones in which this change comes only *through* overt behavior. And let us now apply this in more detail.

We will begin again with trial and error. The cat, it must be noted, learns only *after* she has actually pulled the loop and thus experienced its resultant success. That is, her learned readiness for loop pulling comes only after she has actually done it and experienced its good results, as contrasted with the bad results of the other trials and errors which she also tries as part of her initial array. In other words, we must assume that the learning arises in this type of case only when the relative values of the correct and wrong responses

have actually been demonstrated through trying them out and obtaining actual experiences of their respective good and bad results.

Consider, however, the case of insight learning. When the experiment is a crucial one, when, that is, it is crucially definitive of a so-called "insight" or nontrial and error solution, the response which is finally chosen must *not* be one among the initial array of trials and errors. The ape must have never before, in this sort of a situation, used a stick. The virtue of this stick response must, then, in some way be discovered without, and before, actually trying it. The ape must "foresee" both its possibility and the goodness of its result. Herein, then, would seem to lie the peculiar essence of the primary or insight solution. In it, the new insight arises by "foresight" rather than as a mere by-product of acts after they have been performed.

But there is one point more. In trial and error learning the animal first performs an original array of trials and errors. He finds the result of one of these to be a situation such that (given his innate or acquired endowment) it leads him at once, when actually present, to an appropriate further response. Thus among the original array of the kitten's trials and errors is the pulling of the loop. But this results in the open door. And an open door is a type of situation such that (given the innate or acquired endowment of the cat) it leads at once to the appropriate further response of going out. (An open door in this kind of a problem is a prepotent stimulus situation for the cat.) Also, it is to be noted, that the other responses within the original array are such as to lead to situations for which no such further appropriate responses are in readiness. The unsuccessful bitings and squeezings result in situations which, as such, evoke merely neutral or negative responses. Learning, we shall declare, accrues, then, only in so far as these respective good and bad results become in some way, rapidly or gradually, clearly or dimly, *represented* by the organism to himself at the moments before the acts leading to them are released. For only by assuming such *representations* can we explain that the propensity towards the one act becomes re-enforced while those towards the other acts become weakened.

Take, now, insight learning (or, as we had better perhaps call it from now on, "foresight" learning). By hypothesis the successful act in this case is not one among the array of original trials which are initially ready to go off. How, then, is this act finally hit upon? Again we must assume that the ends of acts can be represented at

moments before those acts are performed. Thus we must assume that the ape is capable of in some way representing (after a certain amount of experience) the resulting spatial gap between its paw and the distant food which results when he actually reaches his paw out. And we shall also assume that he is able to represent the consequent extension of his arm which results when he picks up the stick. And, now, all we have to assume further is that he is capable of *combining these two representations*, in order to explain the appearance of the correct solution. We merely have to assume that at, say, some moment when he is looking at the stick he represents to himself not only the result of picking it up (*i.e.*, his lengthened arm) but also the result of reaching his paw out towards the food. For he will thus achieve the new composite representation of his arm lengthened by stick and this lengthened arm as reaching out towards and making contact with the food. But this new representation presents a situation which, if present, would lead then and there to an appropriate further response—that of raking the food in. (We are assuming, that is, that if the situation of stick-already-in-place were presented, the correct further response of raking it in would not have to be learned, but that it lies within those that an ape is, as such, ready to do;—just as, indeed, in the case of the cat, once the opened door is presented, the further correct response of going out is already within the cat's equipment and prepotently ready.) By dint, then, of some sort of mental play, the ape projects a new situation, *i.e.*, the combined result of a composite act, only the parts of which he has already done and these only separately. And since this represented new situation is one which, if actually presented, would immediately evoke an appropriate further response, he now does the new act leading to it. The new insight arises, in other words, out of an ability to achieve in representation the results of compound acts, only the component parts of which have previously been performed. Foresight learning involves free play among representations:—the ability to add them together (and also in some instances to subtract them) and thus to create new representations. Finally, it should be emphasized, however, that whereas we have thus far for the purposes of exposition stressed this peculiar play of representations (*i.e.*, “foresight”) as distinctive of the ape, in reality we would suppose it also to function in some degree in the case of the cat. It would, in fact, seem to us probable that in so far as an animal can represent the ends of its acts at all (*i.e.*, in so far, indeed, as it can learn), it

can also to some extent combine—add together or subtract—these representations one with another, and thus achieve new representations and the new acts which would lead to them. Indeed, we seem to have an actual illustration of this sort of thing in the case of Higginson's rats (12), who, it will be remembered, took, as soon as they had an opportunity, a new short cut which they had never, as such, previously performed. (This would be a case where the new representation was formed by subtraction among the acts already performed.)

In conclusion, it may be well to tabulate the essential features of learning both of the trial and error and of the insight (or foresight) varieties, as these features have precipitated themselves out from the above discussion.

(1) All learning is to be said to arise out of an initial postulation of (insight into) the goal position, and to end in a new improved, or added to, postulation of (insight into) such goal position.

(2) All learning may be said to involve the representation of the ends of acts at moments before their actual occurrence.

(3) When these represented ends of acts are situations which when actually present lead at once (given the animal's innate and acquired endowment) to further appropriate responses, then the propensities towards the acts leading to those ends will become strengthened.

(4) When, on the other hand, these represented ends of acts are situations which when actually present lead only to negative or avoidance responses, then the propensities towards the acts leading to those ends will become weakened.

(5) The higher the animal, the fewer the number of experiences of an act which are probably necessary to achieve such representations of its end, and the clearer and more accurate such representations themselves probably are.

(6) The higher the animal, the more it would seem that these representations can be played with and manipulated; the more the animal can mentally add and subtract the acts to produce new representations; the more, in short, he can achieve "foresight," as opposed to mere trial and error solutions.

REFERENCES

1. ALONZO, A. S., The Influence of Manual Guidance Upon Maze Learning. *J. Comp. Psychol.*, 1926, 6, 143-157.

2. ANDERSON, J. E., and SMITH, A. H., The Effect of Quantitative and Qualitative Stunting Upon Maze Learning in the White Rat. *J. Comp. Psychol.*, 1926, 6, 337-359.
3. BALL, J., The Female Sex Cycle as a Factor in Learning in the Rat. *Amer. J. Physiol.*, 1926, 78, 533-536.
4. BUYTENDIJK, F. J. J., Considérations de psychologie comparée à propos d'expériences faites avec la singe *Cercopithecus*. *Arch. neerl. de physiol.*, 1921, 5, 42-88.
5. CARR, H. A., *Psychology, A Study of Mental Activity*. Longmans, Green & Co., 1925, p. 98.
6. CARR, H. A., The Reliability of the Maze Experiment. *J. Comp. Psychol.*, 1926, 6, 85-94.
7. DUNCKER, K., A Qualitative (Experimental and Theoretical) Study of Productive Thinking (Solving of Comprehensible Problems). *Ped. Sem.*, 1926, 33, 642-708.
8. GARTH, T. R., and MITCHELL, M. P., The Learning Curve of a Land Snail. *J. Comp. Psychol.*, 1926, 6, 103-114.
9. GOTZ, W., Vergleichende Untersuchungen zur Psychologie des optischen Wahrnehmungsvorgänge. I. Experimentelle Untersuchungen zum Problem der Sehgrößenkonstanz beim Haushuhn. *Zsch. f. Psychol.*, 1926, 99, 247-260.
10. HEMPLEMANN, F., *Tierpsychologie vom Standpunkte des Biologen*. Leipzig, 1926.
11. HERTZ, M., Beobachtungen an gefangenen Rabenvögeln. *Psychol. Forsch.*, 1926, 8, 336-397.
12. HIGGINSON, G. D., Visual Perception in the White Rat. *J. Exp. Psychol.*, 1926, 9, 337-347.
13. HUNTER, W. S., A Reply to Professor Carr on "The Reliability of the Maze Experiment." *J. Comp. Psychol.*, 1926, 6, 393-398.
14. HUNTER, W. S., and RANDOLPH, V., A Note on the Reliability of the Maze as a Method of Studying Learning in the Angora Goat. *Ped. Sem.*, 1926, 33, 3-8.
15. KOCH, H. J., The Influence of Mechanical Guidance Upon Maze Learning. *Psychol. Monog.*, 1923, 32, No. 147.
16. KOFFKA, K., Mental Development. In *Psychologies of 1925*, Clark University, Worcester, 1926.
17. KOFFKA, K., *The Growth of the Mind*. New York, 1925.
18. KROH, O., and SCHOLL, R., Vergleichende Untersuchungen zur Psychologie der optischen Wahrnehmungsvorgänge. II. Ueber die teilinhaltliche Beachtung von Form und Farbe beim Haushuhn. *Zsch. f. Psychol.*, 1926, 100, 260-273.
19. LASHLEY, K. S., Studies of Cerebral Function in Learning. VII. The Relation Between Cerebral Mass, Learning, and Retention. *J. Comp. Neur.*, 1926, 41, 1-58.
20. LASHLEY, K. S., and MCCARTHY, D. A., The Survival of the Maze Habit After Cerebellar Injuries. *J. Comp. Psychol.*, 1926, 6, 423-434.
21. LINDEMANN, E., Untersuchungen über primitive Intelligenzleistungen hochgradig Schwachsinniger und ihr Verhältnis zu den Leistungen von Anthropoiden. *Zsch. f. d. ges. Neur. u. Psychiat.*, 1926, 104, 529-570.

22. LIPMANN, O., Ueber Begriff und Erforschung der "natürlichen" Intelligenz. *Zsch. f. Angew. Psychol.*, 1918, 13, 192-201.
23. LIPMANN, O., and BOGEN, "Naive Physik." Theoretische und experimentelle Untersuchungen über die Fähigkeit zu intelligentem Handeln. Leipzig, 1923.
24. LUDGATE, K. E., The Effect of Manual Guidance Upon Maze Learning. *Psychol. Monog.*, 1924, 33, No. 1.
25. NELIMANN, H., and TRENDLENBURG, W., Ein Beitrag zur Intelligenzprüfungen niederer Affen. *Zsch. f. vergl. Physiol.*, 1926, 4, 142-201.
26. PEISERS, J., Prüfungen höherer Gehirnfunktionen bei Kleinkindern. *Jahrb. f. Kinderheilk.*, 1920, N. F., 91, H. 3, 182.
27. PETERSON, J., The Effect of Length of Blind Alleys on Maze Learning. *Behav. Monog.*, 1917, 3, No. 4.
28. RABAUD, E., Acquisition des habitudes et repères sensoriels chez la guêpe. *Bull. Biol. Fr. & Belg.*, 1926, 60, 319-333.
29. RABAUD, E., L'orientation lointaine et la reconnaissance des lieux. *J. de Psychol.*, 1926, 23, 789-825; 885-924.
30. RÉVÉSZ, G., Experimental Study in Abstraction in Monkeys. *J. Comp. Psychol.*, 1925, 5, 293-341.
31. SCHALLER, A., Sinnesphysiologische und psychologische Untersuchungen an Wasserkäfern und Fischen. *Zsch. f. vergl. Physiol.*, 1926, 4, 370-464.
32. STONE, C. P., and NYSWANDER, D. B., The Reliability of Rat Learning Scores from the Multiple-T Maze as Determined by Four Different Methods. *J. Comp. Psychol.*, 1928, 8 (to appear).
33. THOMPSON, E. L., An Analysis of the Learning Process in a Snail, *Phrya gyrina*, Say. *Behav. Monog.*, 1917, 3, No. 14.
34. TINKLEPAUGH, O. L., *The Delayed Reaction in Monkeys*. Ph.D. Thesis. Univ. of California, May, 1927.
35. TOLMAN, E. C., Purpose and Cognition: The Determiners of Animal Learning. *Psychol. Rev.*, 1925, 32, 285-298.
36. TOLMAN, E. C., Habit Formation and Higher Mental Processes in Animals. *Psychol. Bull.*, 1927, 24, 1-35.
37. TOLMAN, E. C., and NYSWANDER, D. B., The Reliability and Validity of Maze Scores for Rats. *J. Comp. Psychol.*, December, 1927, 7.
38. TRYON, R. C., The Effect of the Unreliability of Measurement on the Difference Between Groups. *J. Comp. Psychol.*, 1926, 6, 449-453.
39. WANG, T. L., The Influence of Tuition in the Acquisition of Skill. *Psychol. Monog.*, 1925, 34, No. 154.
40. WARDEN, C. J., The Distribution of Practice in Animal Learning. *Comp. Psychol. Monog.*, 1922, 1, No. 3.
41. WARDEN, C. J., A Comparison of Different Norms of Mastery in Animal Maze Learning. *J. Comp. Psychol.*, 1926, 6, 159-180.
42. WASHBURN, M. F., Hunger and Speed of Running as Factors in Maze Learning in Mice. *J. Comp. Psychol.*, 1926, 6, 181-188.
43. WHITE, A. E., and TOLMAN, E. C., A Note on the Elimination of Short and Long Blind Alleys. *J. Comp. Psychol.*, 1923, 3, 327-331.
44. WILLIAMS, J. A., Experiments with Form Perception and Learning in Dogs. *Comp. Psychol. Monog.*, 1926, 4, No. 18.

THE PARATHYROIDS

BY JOHN G. ROCKWELL

University of Minnesota

Anatomy. In most species the parathyroids are four in number, two superior and two inferior. Each has its own blood supply. The nerve supply is from the perivascular sympathetic plexus. Little is known of the embryology. Jackson (66, 67, 68), however, has found that their growth energy surpasses that of the thyroid. This author finds that holding animals at a fixed maintenance of body weight the parathyroids increased in size whereas the thyroids suffered reduction.

Histologically, the parathyroids present quite a different picture from the thyroid. Colloid is scarce and the cells tend to arrange themselves in columns, separated by bands of connective tissue. Each gland has a well defined capsule (2, 8, 9, 65, 96, 106, 123).

It has been held that the thyroid and parathyroids are closely related functionally, that the latter are merely embryonic thyroid tissue (118). The beautiful researches done on parathyroid tetany seem to show conclusively that, although their association is an intimate one from the standpoint of location, functionally the two organs are quite distinct (47, 48, 51, 54, 55).

Function. The history of parathyroid research is fascinating. The glands were first adequately described by Sandstroöm, in 1880, who found them present in both man and animal. No great attention was given to the discovery until Gley (54) in 1891 rediscovered them and showed them to be different functionally from the thyroid. Gley, fortunately, worked with the rabbit in which, as we have previously suggested, the external parathyroids are not in intimate contact with the thyroid. He found that when both thyroid and parathyroids were removed, severe and fatal symptoms ensued, similar to those described by Schiff, Rapp, Horsley (106), and others.

Gley, furthermore, showed that when he removed the external parathyroids and left the thyroid no fatal results took place. The same was true when the external parathyroids were left and the thyroid—containing the internal parathyroids—was removed. The explanation seems to be that in many of the vertebrates, the dog, cat, and others, a thyroidectomy means a parathyroidectomy as well.

In 1895, Kohn (78, 79) discovered the internal parathyroids so the explanation of Gley's results was at hand.

The brilliant work of two Italian investigators, Vassale and Generali (115, 116, 117), completed this phase of the problem. Thoroughly acquainting themselves with the glands from an anatomical standpoint, they removed both external and internal parathyroids from nineteen cats and dogs. One of the ten cats survived and all of the dogs were dead in eight days. The picture they presented is identical with that we now term parathyroid tetany. In general it consists in fibrillary twitching and muscular spasms, rigid and uncertain gait, anorexia, tachycardia, emaciation, fall in body temperature, and death. They, furthermore, found that parathyroid-ectomy alone was more rapidly fatal than thyroparathyroidectomy. They advanced a theory of detoxication, arguing as sustaining evidence that parathyroid tetany was less severe in old dogs, less severe also in fasting animals, and more severe in meat fed animals. Here the onset is more rapid and severe than in herbivorous animals or in carnivorous animals whose diets have been carefully controlled. These observations are extremely interesting in light of the recent work that has been done, particularly by Dragsted and his associates (31, 32, 33, 34, 35), and Luckhardt and Rosenbloom (83), whose work will be discussed later.

Thus in the next two decades we find the lead given by Gley, Vassale, and Generali, multiplying itself in extensive research. As is to be expected, there was considerable disagreement about the interpretations of Vassale and Generali. In general two theories shaped themselves: one, that of detoxication advanced by Vassale and Generali, and the other that of a specific secretion of the parathyroids essential to proper bodily maintenance.

Erdheim (40, 41, 42, 43), in 1911, in an elaborate work on the rat noted the prevalence of tetany, and noted particularly that in the surviving animals there were defects in tooth calcification. The influence of diet and age on the ensuing tetany had been observed, and in 1913 Carlson (15) showed the importance of pregnancy as an intensifying factor in tetany (5, 11, 36, 44, 93, 95, 106, 108, 112, 121, 124).

At this point it seems well to return to another line of attack on the problem. Gregor in 1900 had suggested the importance of diet and in 1901 Sabbatani (101) showed that depression of the nervous system can be accomplished by calcium salts. Jacques Loeb (82) had

also shown that the precipitation of calcium salts will increase irritability. Placing a nerve-muscle preparation of a frog in a medium that rendered the calcium inactive he was able to record the character of the muscular responses. The twitchings were depressed with the addition of calcium. Roncoroni (100) demonstrated that reduction of calcium to the cortex may even produce results similar to epilepsy and that these disappear with the introduction of calcium. Analysis was made by Quest on the nervous systems of children dying in tetany, with the result that he found calcium deficient.

In line with this MacCallum and Voegtlin at Hopkins did a very important piece of work using dogs as their experimental animals (36, 87, 88, 89, 90). They found that the injections of soluble calcium salts depressed the tetany and restored the animals to normal condition; and they suggested that parathyroid deficiency is characterized by *calcium deficiency*.

Objections to this theory have taken several forms. In the first place a milk diet—milk being high in calcium content—was said to assist in prevention of tetany, but bone ash, even higher in calcium content, did not materially seem to retard or prevent tetany in dogs. Again, administration of other salts such as strontium, magnesium, etc., seem to be equally effective (7, 73, 107, 120). Lastly, bleeding the animals and substituting a calcium free isotonic solution of sodium chloride also brings an animal out of tetany. Many other objections have been urged. Perhaps the most convincing has come from Dragsted (31, 32, 33, 34, 35) in his work on lactose and the rôle it plays in the control of tetany.

It is doubtful that calcium alone will indefinitely control tetany. Furthermore, there seems to be some adjustment that goes on following parathyroidectomy—perhaps a vicarious functioning of some other organ—so that if an animal survives a few weeks, the prognosis is good. There is, on the other hand, now very suggestive evidence in favor of the calcium theory; the question is by no means closed. Erdheim's work points in this direction, and in line with Erdheim's conclusions is the clinical observation that tetany is more prevalent in rachitic children. The theory of calcium deficiency need not be antagonistic to the detoxication theory. Calcium may have some action on protein; it may combine and render harmless some toxins in the blood. Elimination of calcium in the urine may be the result rather than the cause of tetany.

The toxemia theory suggested by Vassale and Generali has offered

various possibilities in the way of research. MacCallum and Voegtlin noted that ammonia was present in increased quantities in the blood of animals in tetany. Jacobson and Carlson (14, 69, 70, 71) injected ammonia into dogs and cats and were able to produce a condition similar to tetany. These workers carrying their work further, with improved technique for the estimation of blood NH_3 demonstrated that NH_3 content in the blood of parathyroidectomised dogs is not greater than that of normal dogs. They also noted other significant differences between ammonia tetany and parathyroid tetany, *i.e.*, the ammonia dogs show an increased auditory excitability. Sectioning the spinal cord in the upper thoracic region in the parathyroidectomised dogs will abolish the muscular spasms posterior to the lesion; it has no effect on the ammonia treated dogs. There may be decreased as well as increased motor excitability of the motor nerves, or increased motor excitability and decreased sensory.

When the research was extended to a study of the gastrointestinal tract, Carlson concludes that there are "no spasm contractions or other evidence of neuromuscular mechanisms of the digestive tract in parathyroid tetany in cats and dogs. Even in very severe tetany the movements of the stomach and the intestine may be normal. The deviation from the normal is in the direction of depression or paralysis." This depression applies also to the other sympathetic and autonomic mechanisms (cervical sympathetic, pilomotor, sweat nerves, the uterus, the bladder, the sphincters). The explanation seems to be that the depression is due either directly, or indirectly to certain substances in the blood.

Koch (74, 75, 76, 77) in 1912 and 1913 reports the finding of methyl guanidin in the urine of dogs in tetany; and in 1917 Paton(98) enlarges upon this and fixes upon toxemia as the cause of tetany. Guanidin hydrochloride and methyl guanidin nitrate, when injected into animals, produce symptoms identical with those of parathyroid tetany. Burns and Sharpe (102) quantitatively determined the amount of guanidin and methyl guanidin present in normal animals and in animals in tetany. They did the same with normal children and children subject to tetany. Parathyroidectomised dogs yield approximately eight times as much as normal animals, and children subject to tetany show in the active stage .58 mg. per thousand c.c. as against .12 mg. in normal children. Other interesting work has been done on guanidin, work that appeared to be quite suggestive. Parathyroid tetany is characterized by a decrease

in blood calcium, and a consequent disturbance of the acid-base relationship. It was stated that injection of guanidin causes a similar drop of blood calcium. Others have failed to secure this result. Perhaps the most telling criticism against the guanidin theory has come from Collip (18, 19, 20, 21) and his associates. Collip and Clark report having observed guanidin intoxication in dogs coincident with parathyroid hormone overdosage. Parathyroid hormone is a tremendously potent product which Collip has recently isolated from the parathyroids of the ox. This will be discussed in detail later. It has the ability to drive the blood calcium up. If guanidin results in a fall of blood calcium then there should be an antagonism between guanidin and parathyroid hormone. This Collip and Clark have been unable to confirm (106). Similar results are reported by White and Cameron (13). Greenwald (52, 53, 72, 122) failed to demonstrate a toxin in the blood of parathyroidectomised dogs. Such evidence Collip interprets as antagonistic to the *guanidin toxemia theory*. However, some of Luckhardt's work, which will be discussed later, suggests that the toxemia theory has not been entirely disposed of (3, 13, 62, 80, 94, 97, 98, 103, 104, 105, 119, 123).

Uhlenhuth (114) suggests that there is a toxicity from the thymus secretion, to which the parathyroids are antagonistic. He found that if larvae of salamanders were fed on thymus tissue tetany made its appearance, but disappeared with the development of the parathyroids (10).

But we have multiplied at too great length our citations and there remain now three very suggestive series of researches to be discussed. Luckhardt and Rosenbloom (83), in 1922, published the report of a method for the control and cure of parathyroid tetany. This consists literally in washing the animal out by the intravenous injection of large quantities of Ringer's solution. By such a treatment a completely parathyroidectomised dog can be kept alive for an extended period; and after about six weeks is cured of his tetany. Excessive heat, constipation, heavy meat diet—especially if the meat is not fresh—and pregnancy are apt to precipitate an attack. This can be quickly combated by the injection of Ringer's solution. They show that an almost fatal attack of tetany can be brought on thirty-three days after parathyroidectomy by feeding 0.5 of a pound of stale meat. Under this method of control the animals can stand the crucial test of pregnancy, labor, and lactation, with no fatal result. They think the source of the tetany is of exogenous origin, and

comes particularly from meat in the diet. This is clearly a toxemia theory. Luckhardt and Goldberg (84), working with calcium lactate, report that its administration in huge quantities by mouth controls tetany in completely parathyroidectomised dogs. The tetany returns if the treatment is stopped for twenty-four hours (85).

In the same laboratory (Chicago), and at the same time that Luckhardt was carrying on these experiments, Dragsted (31, 32, 33, 34, 35, 99) and his associates were developing a technique for the control of parathyroid tetany by the control of the diet. In general their method consists in pushing a certain diet that is conducive to the cultivation of an aciduric or fermentative type of bacteria in the gut. Such a medium can be obtained by a diet rich in carbohydrates and low in proteins. Dragsted used white bread, milk, and a considerable quantity of lactose. Also, he was able to obtain the same result with boiled rice, beef heart, and lactose. There can be no doubt but that dogs when fed on such a diet withstand parathyroidectomy very much better than do dogs on a stock diet. The experimenters conclude—and their conclusions are in harmony with those of Luckhardt—that parathyroid tetany is due to an intoxication, the responsible agents of which come largely from the intestine. These toxins, in the main, have their origin in the activity of the proteolytic group of intestinal bacteria, and seem to be related to protein split products (1, 4, 5, 63, 109).

A dissenting voice has been raised against Luckhardt's interpretations by Hammett (56). He finds that rats fed for four days on meat, previous to operation, show a lower mortality than do animals on a carbohydrate diet, and concludes that endogenous metabolism and not the meat of the diet is the source of the poisons. One question here whether four days is an adequate time to build up a fermentative medium. Hammett (56, 57, 58, 59) reports that wild animals succumb very much more readily to parathyroid tetany than do animals which are tame, "gentled." Thus, he states that the mortality of "ungentled" rats is 87 per cent as against 13 per cent of the gentled animals. It is true—it has been observed many times—that emotional conditions will precipitate an attack of tetany in an animal that has been parathyroidectomised. It may be true that such conditions lead to an earlier and more certain death, but certainly "gentling" will not keep dogs or cats alive if their total parathyroid apparatus is removed. Furthermore, my observations, based on many hundreds of parathyroidectomised rats, compel me to question

whether tameness or wildness is a very important factor even with rats.

In 1923-1924, Hanson announced that he had been able to isolate a product from the parathyroid glands. This was prepared by a weak acid extract from the parathyroids of cattle. He tested this product on experimental tetany in animals and in man (39, 60, 61). In 1924, Collip (18, 19, 20, 21, 30, 37, 38, 45, 46, 50, 64, 91, 92, 110, 111, 114), by weak acid hydrolysis of the fresh or acetone preserved ox parathyroids, isolated a very potent substance which he thinks contains the actual physiological product of the glands. As mentioned before, parathyroid tetany manifests a disturbed acid base relationship in the blood, and is characterized by a striking decrease in blood calcium. This substance of Collip prevents or relieves tetany in dogs, and has even been put to a very crucial test—that of relieving tetany in young dogs on a meat diet. It has long been known that young animals are more susceptible than older animals, and meat feeding has from the days of Vassale and Generali been known to accentuate the condition.

This product has been studied very extensively both on normal and parathyroidectomised animals. Dogs and cats are very sensitive to injections of the hormone. Rats, rabbits, and guinea pigs are more resistant. With the former animals, there is great danger of overdosage which results in death. With the latter animals, this is not so true. Once tetany comes on, the hormone is not so effective in rabbits. However, it does control the tetany provided the treatment is started immediately after the operation. Particularly interesting are the results with dogs. The effects on normal dogs are the same as on thyro-parathyroidectomised dogs. This suggests that these organs, the thyroid and parathyroids, although in such intimate contact with one another, are entirely distinct in function. Neither has any influence on the other. This is an answer to the old claim that the parathyroids are simply embryonic thyroid tissue (12, 13, 17, 18, 19, 22, 23, 24, 25, 26, 27, 28, 29).

The clinical applications of the hormone are being undertaken. Some reports are available now, and we may expect that Collip will from time to time summarize the results (6).

Interest in the problem of parathyroid tetany urges one to speculate on whether there is a possible relationship with other forms of tetany clinically seen, spasmophilia, eclampsia, occupational tetany, and epilepsy. Many medical writers have long insisted that the

mental deficiency so frequently present in epilepsy is the result of the disease and not a concomitant condition. Psychologists at the present time need to be a little cautious in extending a theory of hereditary determinism to the various kinds of mental deficiency. Hereditable—yes! But uncontrollable? This is still an open question.

BIBLIOGRAPHY

1. ALDBERG, E. and IVY, A. C., The Effect of Colectomy on the Incidence of Parathyroid Tetany. *Am. J. Physiol.*, 1926, **76**, 226.
2. BERGSTRAND, H., Parathyreoideastudien. Quoted from *Physiological Abstracts*, 1921-22, 1888. *Acta Med. Scand.*, 1920, **52**, 791-855. 1921, **54**, 539-600.
3. BERMAN, L., The Effect of a Protein Free Acid Alcohol Extract of the Parathyroid Glands Upon the Calcium Content of the Blood, and the Electrical Irritability of the Nerves of the Parathyroidectomised and Normal Animals. *Am. J. Physiol.*, 1926, **75**, 358-65.
4. BIKOV, K. M., and SAVITCH, V. V., The Effect of Dietary Conditions on Tetany. (Quoted from *Physiological Abstracts*, November, '24.) *Russ. Arch. Biol. Sci.*, 1923, **23**, 129-36.
5. BLUMENSTOCK, J., TWEEDY, W. R., and BRANNON, L., Additional Observations of Eck Fistula Thyro-parathyroidectomised Dogs. *Am. J. Physiol.*, 1926, **76**, 194-5.
6. BOOTHBY, W. M., Parathyroids. *Endocrinology*, 1921, **5**, 403-40.
7. BOYT, T. E., AUSTIN, W. C., and DUCEN, E. F., Attempts to Control Parathyroid Tetany by the Oral Administration of Ammonium Chloride. *Am. J. Physiol.*, 1926, **77**, 225-32.
8. BRODSKY, J., Die Heteroplastik der Endokrinen Drüsen bei Erkrankungen des Nervensystems (Heteroplasty of Endocrine Glands in Diseases of the Nervous System). (Quoted from *Physiological Abstracts*, November '25.) *J. f. Psychol. u. Neurol.*, 1923-24, **30**, 77-86.
9. CAMERON, A. T., and CARMICHAEL, J., Acceleration of Growth and Regression of Organ Hypertrophy in Young Rats after Cessation of Thyroid Feeding. Production of Tetany by Thyroid Feeding. *Trans. R. Soc. Can.*, 1922, **16**, 57-70.
10. CAMERON, A. T., and CARMICHAEL, J., A Note on Tetany in Thyroid Fed Rats and the Supposed Antagonism between Thymus and Parathyroid. *Trans. Roy. Soc. Can.*, 1925, **19**, 53-56.
11. CAMERON, A. T., and CARMICHAEL, J., Sudden Atmospheric Changes as Contributory Factors in the Production of Tetany. *Trans. Roy. Soc. Can.*, 1926, **20**, 277-96.
12. CAMERON, A. T., and MOORHOUSE, V. H. K., The Action of Collip's Parathyroid Extract on Blood and Cerebro-Spinal Fluid Calcium. *Trans. Roy. Soc. Can.*, 1925, **19**, 39-43.
13. CAMERON, A. T., and MOORHOUSE, V. H. K., The Tetany of Parathyroid Deficiency and The Calcium of the Blood and Cerebro-Spinal Fluid. *J. Biol. Chem.*, 1925, **63**, 687-720.

14. CARLSON, A. J., and JACOBSON, C., Further Studies on the Nature of Parathyroid Tetany. *Am. J. Physiol.*, 1911, **28**, 133-160.
15. CARLSON, A. J., The Parathyroids and Pregnancy. *Proc. Soc. Exp. Biol. & Med.*, 1913, **10**, 183-84.
16. CLARK, G. A., Inter-relation of the Parathyroids, Suprarenals, and Pancreas. *J. Physiol.*, 1924, **58**, 294-301.
17. CANTAROW, A., CAVEN, W. R., and GORDON, B., Changes in the Chemical and Physical Characteristics of the Blood following the Administration of Parathyroid Hormone. *Arch. Int. Med.*, 1926, **38**, 502.
18. COLLIP, J. B., The Extraction of a Parathyroid Hormone which will Prevent or Control Parathyroid Tetany and which Regulates the Level of the Blood Calcium. *Biol. Chem.*, 1925, **63**, 395-438.
19. COLLIP, J. B., The Internal Secretion of the Parathyroid Glands. *Proc. Nat. Acad. Sc.*, Washington, 1925, **11**, 484.
20. COLLIP, J. B., A Parathyroid Hormone and its Physiological Action. *Am. J. Physiol.*, 1925, **72**, 182-3.
21. COLLIP, J. B., The Parathyroid Glands. *The Harvey Lectures*, 1925-26.
22. COLLIP, J. B., The Production of Some of the Phenomenon Peculiar to Parathyroid Overdoses in Dogs by Means of Certain Inorganic Salts. *Am. J. Physiol.*, 1926, **76**, 472-82.
23. COLLIP, J. B., A Study of Parathyroidectomised Rabbits. *Am. J. Physiol.*, 1926, **76**, 219.
24. COLLIP, J. B., Concerning the Relation of Guanidine to Parathyroid Tetany. *J. Biol. Chem.*, 1926, **67**, 679-87.
25. COLLIP, J. B., and CLARK, E. P., Further Studies on the Physiological Action of a Parathyroid Hormone. *J. Biol. Chem.*, 1925, **64**, 485-507.
26. COLLIP, J. B., and CLARK, E. P., Further Studies on the Parathyroid Hormone. *J. Biol. Chem.*, 1926, **66**, 133-137.
27. COLLIP, J. B., and CLARK, E. P., and SCOTT, J. W., The Effect of a Parathyroid Hormone on Normal Animals. *J. Biol. Chem.*, 1925, **63**, 439-60.
28. CRUICKSHANK, E. W. H., Studies in Experimental Tetany. III, On Alkalosis and Acidosis. IV, On the Hydrogen-Ion Concentration of the Blood. V, On the Alveolar Carbon Dioxide Tension. *Biochem. J.*, 1924, **18**, 47-62.
29. CRUICKSHANK, E. W. H., Studies in Experimental Tetany. I, On the Distribution of Calcium in the Plasma and Cells. II, On the Variations in Colloidal and Ionic Calcium. *Biochem. J.*, 1923, **17**, 13-28.
30. DAVIES, D. T., DICKENS, F., and DODDS, E. C., Observations on The Preparation, Properties and Source of the Parathyroid Hormone. Part I. *Biochem. J.*, 1926, **20**, 695-702.
31. DRAGSTED, L. R., and PEACOCK, S. C., Studies on the Pathogenesis of Tetany. *Am. J. of Physiol.*, 1923, **64**, 424-34.
32. DRAGSTED, L. R., PHILLIPS, K., and SUDAN, A. C., Studies on the Pathogenesis of Tetany. II, The Mechanism Involved in Recovery from Parathyroid Tetany. *Am. J. Physiol.*, 1923, **65**, 368-78.
33. DRAGSTED, L. R., PHILLIPS, K., and SUDAN, A. C., Studies on the Pathogenesis of Tetany. III, Exciting factors in Experimental Tetany in Dogs. *Am. J. Physiol.*, 1923, **65**, 503.

34. DRAGSTED, L. R., Further Studies on Parathyroid Tetany. *Am. J. Physiol.*, 1925, 72, 205.
35. DRAGSTED, L. R., and SUDAN, A. C., Studies on the Pathogenesis of Tetany. V, The Prevention and Control of Parathyroid Tetany by Calcium Lactate. VI, The Prevention and Control of Parathyroid Tetany by Strontium. VII, The Prevention and Control of Parathyroid Tetany by the Oral Administration of Kaolin. VIII, The Effect of Guanidine Intoxication on the Blood Calcium of Parathyroidectomised Dogs. *Am. J. Physiol.*, 1926, 77, 296-306, 307-13, 314-20, 321-25.
36. DRUCKER, P., and FABER, F., Investigations in Tetany. *J. Biol. Chem.*, 1926, 68, 57.
37. EDWARDS, D. J., and PAGE, I. H., Effects of Parathyroid Extracts on the Heart and Circulation. *Am. J. Physiol.*, 1926, 78, 235-45.
38. EDWARDS, D. J., and PAGE, I. H., Some Effects of Parathyroid Extract (Collip) on Heart Function. *Am. J. Physiol.*, 1926, 76, 207-8.
39. ELLINGSON, E. O., BELL, A. W., and HANSON, A. M., Experiments with an Active Extract of Parathyroid. *Proc. Soc. Exp. Biol. and Med.*, 1924, 21, 239-40.
40. ERDHEIM, J., Tetania Parathyreopriva. *Mitt. a. d. Grenzgeb. d. Med. u. Chir.*, 1906, 16, 632.
41. ERDHEIM, J., Über Epithelkörperchenbefunde bei Osteomalazie. *S: Kjunigsb. d. k. Acad. d. Wissensch.* Wien, 1907, 311. *Matt-naturw. Cl.*
42. ERDHEIM, J., Morphologische Studien über die Bezie der Epithelkörperchen zum Kalkstoffwechsel, I. *Frankf. Ztschr. f. Path.*, 1911, 7, 176.
43. ERDHEIM, J., Morphologische Studien über die Beziehung der Epithelkörperchen zum Kalkstoffwechsel, V. *Frankf. Ztschr. f. Pathol.*, 1911, 7, 295.
44. FALTA, *Endocrine Diseases*. P. Blakiston's Son & Co., Philadelphia. 1923.
45. FISHER, N. F., and LARSON, E., Effects produced by Extracts of Parathyroid Glands on Normal and Parathyroidectomised Dogs. *Am. J. Physiol.*, 1925, 75, 93-106.
46. FISHER, N. F., and LARSON, E., Experiments with Extracts of Parathyroid Glands. *Proc. Soc. Exp. Biol. and Med.*, 1925, 22, 447-8.
47. FORSYTH, D., Observations on the Parathyroids and Accessory Thyroids in Man. *Brit. Med. J.*, 1902, 1, 372-373.
48. FORSYTH, D., The Comparative Anatomy, Gross and Minute, of the Thyroid and Parathyroids in Mammals and Birds. *J. Anat. Physiol.*, 1908, 42, 141-168, 302-318.
49. FRANK, E., and KÜHMAN, J., Isolierung von Methylierten Guanidin aus dem Harn Zweier Fälle von Parathyreopriver Tetanie (Isolation of Methylated Guanidine from Urine in Tetania Parathyroiopriva). (Quoted from Physiological Abstracts, Nov. '25.) *Klin. Wchnsch.*, 1925, 4, 1170-1.
50. GRANT, J. H. B., and GATES, F. L., Some Factors Effecting the Levels of the Serum Calcium and Phosphorus of Normal Rabbits. *Proc. Soc. Exp. Biol. and Med.*, 1925, 22, 315-317.
51. GRANT, J. H. B., and GATES, F. L., The Effect on the External Parathyroid Glands of the Exposure of Rabbits to Ultra-Violet Rays. *J. Gen. Physiol.*, 1924, 6, 635-645.

52. GREENWALD, I., Are Guanidines Present in the Urines of Parathyroidectomised Dogs? *J. Biol. Chem.*, 1924, **59**, 329-37.
53. GREENWALD, I., and GROSS, J., The Effect of Long-Continued Administration of Parathyroid Extract Upon the Excretion of Phosphorus and Calcium. *J. Biol. Chem.*, 1926, **68**, 325-33.
54. GLEY, E., Sur les effets de l'extirpation du corps thyroïd. *Comptes rend. Soc. de Biol.*, 1891, **3**, 551, 841, 843. *Arch. de Physiol. norm, and path.*, 1892, **93**, 97.
55. HALPENNY, J. and GUNN, J. A., Note on the Extirpation of the thyroid Gland in Monkeys. *Quart. J. Exp. Physiol.*, 1911, **4**, 237-241.
56. HAMMETT, F. S., The Stability of the Nervous System as a Factor in the Resistance of the Albino Rat to the Loss of the Parathyroid Secretion. *Am. J. Physiol.*, 1921, **56**, 176-204.
57. HAMMETT, F. S., Studies of the Thyroid Apparatus. IX. The Effect of the Loss of the Thyroid and Parathyroid Glands at 100 Days of Age on the Growth in Body Length, Body Weight, and Tail Length of Male and Female Albino Rats. *Am. J. Physiol.*, 1923, **63**, 218-244.
58. HAMMETT, F. S., Rickets and Parathyroids. *Endocrin.*, 1924, **8**, 557-60.
59. HAMMETT, F. S., Studies of the Thyroid Apparatus. XXXVIII, The Relation of the Thyroid and the Parathyroids to the Glands of Internal Secretion. *Endocrin.*, 1926, **10**, 385-404.
60. HANSON, A. M., The Hormone of the Parathyroid Gland. *Proc. Soc. Exp. Biol. and Med.*, 1925, **22**, 560-1.
61. HANSON, A. M., Active Preparations of the Parathyroids. *Mil. Surg.*, 1924, **55**, 701-18.
62. HERXHEIMER, G., Analogisierung der Guanidivirgftung mit der Parathyreopriven Tetanie (Comparison of Tetany due to Guanidine Poisoning with that Following Extirpation of the Thyroids). (Quoted from Physiological Abstracts, May, '25). *Deutsch. Med. Woch.*, 1924, **43**, 1465.
63. HJORT, A. M., The Influence of Orally Administered Calcium Salts on the Serum Calcium of Normal and Thyreoparathyropriva Dogs. *J. Biol. Chem.*, 1925, **65**, 783-95.
64. HJORT, A. M., ROBINSON, S. C., and TENDICK, F. H., An Extract Obtained from the External Bovine Parathyroid Glands Capable of Inducing Hypercalcemia in Normal and Thyreoparathyropriva Dogs. *J. Biol. Chem.*, 1925, **65**, 117-28.
65. HOSKINS, M. M., and CHANDLER, S. B., Accessory Parathyroids in the Rat. *Anat. Rec.*, 1925, **30**, 95-8.
66. JACKSON, C. M., On the Prenatal Growth of the Human Body and the Relative Growth of the Various Organs and Parts. *Am. J. Anat.*, 1909, **9**, 119-165.
67. JACKSON, C. M., Post Natal Growth and Variability of the Body and of the Various Organs in the Albino Rat. *Am. J. Anat.*, 1913-14, **15**.
68. JACKSON, C. M., Effects of Inanition Upon the Structure of the Thyroid and Parathyroid Glands of the White Rat. *Am. J. Anat.*, 1916, **19**, 305-352.

69. JACOBSON, C., The Concentration of Ammonia in the Blood of Dogs and Cats Necessary to Produce Ammonia Tetany. *Am. J. Physiol.*, 1910, 26, 407-412.
70. JACOBSON, C., The Effects of Blood Transfusion in Parathyroid Tetany. *Am. J. Physiol.*, 1912-13, 30, 47-55.
71. JACOBSON, C., The Direct Influence of the Blood of Parathyroid Tetany Animals on the Excitability of the Motor Nerves. (Quoted from Physiological Abstracts, May, '23).
72. JOHKERS, C. H., and REVERS, F. E., Einfluss einer Kalkreichen Nahrung und die Krankhaften Symptome beim Hunde nach partieller Parathyroid extirpation (Calcium Feeding and the Parathyroidectomised Dog). (Quoted Physiol. Abstracts, May, 1925.) *Ztschr. f. Physiol. Chemie*, 1925, 144, 181-9.
73. JUNG, F. T., and COOK, F., Effect of Intraperitoneal Magnesium Sulphate on Parathyroidectomised Rats. *Proc. Soc. Exp. Biol. and Med.*, 1924, 24, 586-587.
74. KOCH, W. F., On the Occurrence of Methyl Guanidine in Urine of Parathyroidectomised Animals. *J. Biol. Chem.*, 1912-13, 12, 313-315.
75. KOCH, W. F., Toxic Bases in the Urine of Parathyroidectomised Dogs. *J. Biol. Chem.*, 1913, 15, 43-63.
76. KOCH, W. F., Physiology of the Parathyroid Glands. *J. Lab. and Clin. Med.*, 1916, 1, 299-315.
77. KOCH, W. F., Tetany and the Parathyroid Glands. *Med. and Surg.*, 1918, 2, 9-17.
78. KOHN, A., Studien über die Schilddrüse. *Arch. f. Mikr. Anat.*, 1895, 44, 366-422.
79. KOHN, A., Die Epithelkörperchen. *Ergebn. der Anat. u. Entwicklsgesch.*, 1899, 9, 129-252.
80. KÜHNAN, J., Isolierung von methylierten guanidinen aus dem Harn zweier Fälle von parathyreopriver Tetanie (Isolation of Methylated Guanidine in Two Cases of Tetany Following Removal of Goiter). (Quoted Physiol. Abstracts, April, 1926.) *Arch. f. Exp. Path. u. Pharmak.*, 1925, 110, 76-88.
81. LEE, M. O., Studies on the Oestrous Cycle in the Rat. II. The Effect of Thyroparathyroidectomy and Parathyroidectomy. *Endocrin.*, 1926, 10, 43-55.
82. LOEB, J., On an Apparently New Form of Muscular Irritability Produced by Solution of Salts Whose Anions Are Liable to Form Insoluble Calcium Compounds. *Am. J. Physiol.*, 1901, 5, 352-373.
83. LUCKHARDT, A. B., and ROSENBLUM, P. J., Control and Cure of Parathyroid Tetany in Normal and Pregnant Animals. *Science*, 1922, 56, 48-49.
84. LUCKHARDT, A. B., and GOLDBERG, B., Preservation of the Life of Completely Parathyroidectomised Dogs. *J. Am. Med. Assoc.*, 1923, 80, 79-80.
85. LUCKHARDT, A. B., WAND, R. O., and BRANNON, L., On the Prevention of Parathyroid Tetany by the Oral Administration of Magnesium Chloride. *Am. J. Physiol.*, 1926, 76, 228.

86. MACCALLUM, W. G., Die Beziehung der Parathyroiddrüsen zur tetanie. *Centralblatt. f. allg. Path.*, 1905, **76**, 385.
87. MACCALLUM, W. G., and DAVIDSON, C. F., Further Notes on the Function of the Parathyroid Glands. *Med. News*, 1905, **86**, 625-33.
88. MACCALLUM, W. G., and VOEGTLIN, C., On the Relation of Tetany to the Parathyroid Glands and to Calcium Metabolism. *J. Exp. Med.*, 1909, **11**, 149.
89. MACCALLUM, W. G., and VOGEL, K. M., Further Experimental Studies in Tetany. *J. Exp. Med.*, 1913, **18**, 618-650.
90. MACCALLUM, W. G., LAMBERT, R., and VOGEL, K., The Removal of Calcium from the Blood by Dialysis in the Study of Tetany. *J. Exp. Med.*, 1914, **20**, 149-168.
91. MACLEOD, J. J. R., Observations Upon the Effects Produced in Normal and Parathyroidectomised Dogs and Herbivorous Animals by Injections of Parathyroid Extract. *Trans. Roy. Soc. Can.*, 1925, **19**, 27-38.
92. MAJOR, R. H., and BINKSTRA, C. R., The Effect of Parathyroid Extract and Liver Extract on the Hypertension Produced by Guanidine Compounds. *Bull. Johns Hopkins Hosp.*, 1925, **37**, 392.
93. MASSAGLIA, A. C., The Internal Secretion of Sandström's Glands. Parathyroid Hyperfunction and Eclampsia. *Endocrin.*, 1921, **5**, 309-24.
94. NELKEN, L., Über den Einfluss der Guanidinvergiftung auf den Ca und Phosphatgehalt des Blutes. (Quoted from Physiological Abstracts.) *Zeit. f. d. ges. exp. Med.*, 1923, **32**, 348-59.
95. NICKOLAS, J. S., and SWINGLE, W. W., Parathyroid Extirpation in the Cat. *Proc. Soc. Exp. Biol. and Med.*, 1923, **21**, 160.
96. NONIDIZ, J. F., and GOODALE, H. D., Histological Studies on the Endocrines of Chickens Deprived of Ultra-violet Light. 1. Parathyroids. *Am. J. Anat.*, 1927, **38**, 319-48.
97. POLLADIN, A., and GRILLICHES, L., Zur der Biochemie der Experimentellen Tetanie. Harn- und Muskelkreatin bei der Guanidin und parathyreoopriven Tetanie ohne und nach Ca-Behandlung. *Biochem. Zeit.*, 1924, **146**, 458-66.
98. PATON, D. N., The Significance of Guanidine in the Animal Body. *Glasgow Med. J.*, 1925.
99. PEACOCK, S. C., and DRAGSTEDT, L. R., The Influence of Parathyroidectomy on Gastric Secretion. *Am. J. Physiol.*, 1923, **64**, 499-502.
100. RONCORONI, L., Alcune esperienze intorno all'azione del calcio sulla corteccia cerebrale. *Riv. sper. di fren.*, 1903, **29**, 157-171.
101. SABBATONI, L., Importanza del calcio che trovasi nella corteccia cerebrale. *Riv. sper. di fren.*, 1901, **27**, 946.
102. SHARPE, J. S., The Guanidine Content of Faeces in Idiopathic Tetany. *Bio-chem. J.*, 1919, **14**, 46-47.
103. SALVESON, H. A., Studies on the Physiology of the Parathyroids. *Proc. Soc. Exp. Biol. and Med.*, 1923, **20**, 204.
104. SALVESON, H. A., and LINDER, G. C., The Relation Between Calcium and Protein of Serum in Tetany Due to Parathyroidectomy. *J. Biol. Chem.*, 1923, **58**, 635-9.
105. SALVESON, H. A., The Function of the Parathyroids. *J. Biol. Chem.*, 1923, **56**, 443-56.

106. SIMPSON, S., Physiology, Physiological Chemistry and Experimental Pathology of the Parathyroid Glands. Barker, *Endocrinology and Metabolism*, D. Appleton & Co., 1922.
107. SLOAN, J. H., On the Mechanism of Prevention of Fatal Parathyroid Tetany by the Oral Administration of Magnesium Chloride. *Am. J. Physiol.*, 1926, **79**, 100-11.
108. SPADOLINI, J., Sulla tetania e sulle alterazioni delle ghiandole paratiroidi nelle avitaminosi e nelle lesioni sperimentali dei nervi mesenterici. (Quoted from Physiological Abstracts, May 24.) *Arch. di fisiol.*, 1923, **21**, 369-77.
109. SPADOLINI, J., Ricerche sulla patogenesi della tetania. I. L'influenza della dieta sulla tetania di animali operati di estirpazione dei nervi mesenterici e di animali mantenuti a regime avitaminico. II. Manifestazioni tetaniche in animali che hanno subito ampie distruzioni della mucosa intestinale. (Quoted from Physiological Abstracts, Nov. 25.) *Arch. di fisiol.*, 1924, **22**, 417-27.
110. STEWART, C. P., and PERCIVAL, G. H., Studies on Calcium Metabolism. I. The Action of the Parathyroid Hormone on the Calcium Content of the Serum and on the Absorption and Excretion of Calcium. *Biochem. J.*, 1927, **21**, 301-313.
111. STEWART, C. P., and PERCIVAL, G. H., The Effect of Administration of Parathyroid on the Serum Calcium. *Quar. J. Med.*, 1927, **20**, 349-52.
112. SWINGLE, W. W., and NICHOLAS, J. S., Autoplastic and Homoplastic Parathyroid Transplantation. *Am. J. Anat.*, 1925, **36**, 91-130.
113. SWINGLE, W. W., and WENNER, W. F., The Effect of Bleeding Upon the Serum Calcium of Thyroparathyroidectomised Dogs. The Prevention and Cure of Tetany by Oral Administration of Strontium. *Am. J. Physiol.*, 1926, **75**, 372-7, 378-9.
114. UHLENHUTH, E., Parathyroids and Calcium Metabolism. *Proc. Soc. Exp. Biol. and Med.*, 1918, **16**, 30-1.
115. VASSALE, G., and GENERALI, F., Sur les effets de l'extirpation des glandes parathyroides. *Arch. ital. de biol.*, 1896, **25**, 459-464.
116. VASSALE, G., and GENERALI, F., Sur les effets de l'extirpation des glandes parathyroïdiennes. *Arch. ital. de biol.*, 1896-7, **26**, 61-65.
117. VASSALE, G., and GENERALI, F., Fonction parathyroïdienne et fonction thyroïdienne. *Arch. ital. de biol.*, 1900, **33**, 154-156.
118. VINCENT, S., and JOLLY, W. A., Some Observations on the Functions of the Thyroid and Parathyroid Glands. *J. Phys.*, 1905, **32**, 65-86; 1906, **34**, 295-305.
119. WATANABE, C. K., Studies in the Metabolic Changes Induced by the Administration of Guanidine Bases. V. The Change of Phosphate and Calcium Content in Serum in Guanidine Tetany and the Relation Between the Calcium Content and Sugar in the Blood. *J. Biol. Chem.*, 1918, **36**, 531-45.
120. WENNER, W. F., The Prevention and Cure of Tetany by Oral Administration of Magnesium Lactate. *Proc. Soc. Exp. Biol. and Med.*, 1926, **23**, 432-4.

121. WENNER, W. F., and MUNTWYLER, E., Hydrogen-ion Concentration and Carbon Dioxide Content of Blood of Parathyroidectomised Dogs. *Proc. Soc. Exp. Biol. and Med.*, 1927, **24**, 480-82.
122. WHITE, F. D., and CAMERON, A. T., The Action of Parathyroid Extracts on Guanidine. *Trans. Roy. Soc. Can.*, 1925, **19**, 45-52.
123. WOODMAN, D., The Effect of Parathyroid Feeding on the Thyroid. *J. Physiol.*, 1926, **61**, 557-61.
124. YOSHIMOTO, M., The Action of the Blood-serum of Animals in Tetania Thyreopriva on Motor Nerve and Striated Muscle. *Quart. J. Exp. Physiol.*, 1922, **13**, 41-52.

